

Vol. VI, No. 4

April, 1920

THE ANNALS OF APPLIED BIOLOGY

THE OFFICIAL ORGAN OF THE ASSOCIATION
OF ECONOMIC BIOLOGISTS

EDITED BY

E. E. GREEN, Way's End, Camberley (late Government Entomologist, Ceylon)

WITH THE ASSISTANCE OF THE COUNCIL



CAMBRIDGE UNIVERSITY PRESS

C. F. CLAY, MANAGER

LONDON: FETTER LANE, E.C. 4

also

H. K. LEWIS & CO., LTD., 136, GOWER STREET, LONDON, W.C. 1

WILLIAM WESLEY & SON, 28, ESSEX STREET, LONDON, W.C. 2

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ASSOCIATION OF ECONOMIC BIOLOGISTS.

At a meeting of the Council of the Association of Economic Biologists held on February 4th, a memorandum was submitted by the Botanical Secretary. This proposed certain reconstructions in the Association and the taking of steps to inaugurate some measure of federation or amalgamation among existing biological societies. The council appointed a sub-committee consisting of Professor V. H. Blackman, Mr W. B. Brierley, Mr F. J. Chittenden and Dr A. D. Imms to consider these proposals. On March 17th a report was presented by the sub-committee and the council ordered that this be printed and circulated with the present number of the *Annals of Applied Biology*.

Report of the sub-committee appointed to consider the proposals submitted to the Council by the Botanical Secretary.

Members. V. H. BLACKMAN, W. B. BRIERLEY, F. J. CHITTENDEN, A. D. IMMS.

Sections. That, in view of the comparatively small number of members the Association contains, it is as yet inadvisable to divide the society into sections.

Meetings.

I. KIND. That meetings should ordinarily include papers dealing with related subjects, grouped, as shown below, (a), (b), (c), but they should sometimes be arranged for the discussion of wider problems common to several branches of biological work. As far as possible these meetings should be held alternately.

- (a) Microbiological subjects including protozoology; bacteriology; mycology; algology; plant and animal disease; fermentation processes, etc.
- (b) General botanical subjects including trees, crop and horticultural plants; problems in applied ecology such as waste land and shore reclamation; timbers; fibres; vegetable drugs and dyes; food values; coal, etc.
- (c) General zoological subjects including entomology; helminthology; animal products; fisheries, etc.

II. NUMBER. That the number of meetings be increased to 8 or 10 per annum, be held on Fridays, and that five be held this year. That the dates of meetings be as follows:

Wednesday, March 24th (as already arranged by Council).

Friday, June 4th.

„ Sept. 24th.

„ Nov. 5th.

„ Dec. 10th.

Duration of meeting—one day.

That the dates of meetings be printed on a card and circulated to members at the beginning of each year.

III. PLACE. That in view of the increased number of meetings these be held in various places. That as most of the present members of the Association live in the southern and midland counties the following places are suggested:

Rothamsted, Kew, Wisley, Merton, London (Imperial College, University College, King's College, R.H.S. Vincent Square), Birmingham, Cambridge, Oxford.

IV. INVITATIONS. That invitations to attend Association meetings be sent to the following organisations: Farmers' Club; Royal Horticultural

Society; Royal Agricultural Society; Royal Arboricultural Society; Agricultural Educational Association; Horticultural Educational Association; Entomological Society; Linnean Society.

- V. JOINT MEETINGS. That where desirable joint meetings with other organisations be arranged. That the Association take an active share in the Potato Conference which the Royal Horticultural Society have in view.

Working Committees.

That small Working Committees be nominated by the Council to consider and report upon special problems or to formulate lines of development of research or to co-ordinate research already in progress. That these Committees report to the Council who will recommend presentation of the report at a General Meeting of the Association and publication in the proceedings.

That these Committees be appointed as needs arise and that any member of the Association may request the Council to appoint a Committee to consider any special matter.

The Sub-Committee recommend that such a Working Committee be appointed forthwith to consider the question of the standardisation of sprays and suggest that the following Members be asked to serve: Mr Fryer, Professor Lefroy, Mr Theobald, Professor Barker, Mr Cotton, Mr Salmon.

That a Committee be appointed to consider the problem of Wart Disease and that the following Members be asked to serve: Professor V. H. Blackman, Mr Brierley, Dr E. J. Russell, Mr Snell.

That Working Committees possess the power to co-opt other Members.

Programmes of Research.

With a view to the co-ordination of research that each year the heads of departments be requested to provide a list of their research workers with a statement of the problems on which they are engaged, and that such lists be published in the Annals.

Membership.

That members nominating persons for admission to the Association be required to fill in the following queries: (1) Name in full. (2) Occupation and position. (3) Professional and private address. (4) Qualifications. (5) Publications. That special membership forms be printed.

Inter-Organisation of Biological Societies.

That in view of the nature of most biological societies, and particularly of their inclusion of and dependence upon amateur members, it would not at present seem feasible to take direct steps toward any scheme of amalgamation or federation. That this ideal be always retained in view and that wherever possible indirect steps be taken to this end. That by joint action with other organisations and active co-operation in meetings, etc., and by the vigorous promulgation of the Association and its ideals much may be achieved in this direction.

NOTE

By invitation of Dr E. J. Russell, F.R.S., the Meeting of the Association on June 4th will be held at the Rothamsted Experimental Station, Harpenden; and it is expected that the Members of the Imperial Entomological Conference will attend.

By invitation of Sir David Prain, C.M.G., F.R.S., the Meeting of the Association on September 24th will be held at the Royal Botanic Gardens, Kew. A conference on the problems of susceptibility or immunity to disease in plants will be arranged for this date.

ON THE RELATIONS BETWEEN GROWTH AND THE ENVIRONMENTAL CONDITIONS OF TEMPERATURE AND BRIGHT SUNSHINE.

By WINIFRED E. BRENCHLEY, D.Sc.

(Rothamsted Experimental Station.)

(With 13 Text-figures.)

It is fully recognised that the amount of growth made by any crop in the field and the rate at which maturity is reached is influenced by many factors such as temperature, rainfall, season, sunlight, soil conditions and available plant food. There is, however, little definite information as to the influence of each of these factors on a plant at various stages of growth nor with regard to the changes in the actual rate of growth at different periods from the seedling to the mature plant.

It is difficult or even impossible to gain this information from crops growing under normal conditions in the field, because some of the factors cannot even be measured with any degree of accuracy and all are so intimately associated that the action of one or other can hardly be disentangled from the rest. Simplification is therefore essential and some method must be adopted whereby certain of the factors are controlled and kept as constant as possible, thereby reducing the number of the variable influences to be observed. The method of water culture was therefore used, as it enables a strict control to be placed on the food and water supplied, it permits of the roots being observed and weighed with far greater accuracy than in soil experiments, and its compactness allows of a large number of plants to be given individual treatment at the same time. It is also possible to keep a close watch on the temperature variations to which the plants are subjected and to observe the effect of these variations on a number of individuals at different stages of growth.

ENVIRONMENTAL CONDITIONS.

The experiments were carried out in a roof greenhouse specially constructed for water culture work and extended over a period of sixteen months from September 1915 to January 1917. As Rothamsted

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is situated in a country district away from the fogs that are common to urban areas the light conditions were good for any given period of the year. This is an important point, as Gregory¹, in experiments on cucumbers at Cheshunt, near London, has shown that with high temperatures light becomes a limiting factor, *i.e.* although other conditions are favourable the growth is limited by the deficiency of light. Artificial heating was installed and the minimum temperatures were kept above freezing point throughout the winter months so that the results, so far as they refer to the effect of minimum temperatures, are only applicable in cases where the latter do not fall below 32° F. Throughout the period the maximum and minimum temperatures were recorded daily except on Sundays, but as the thermometers were read at 9 a.m., the Monday readings included those for both the preceding days, thus insuring that a high maximum or low minimum on Sunday was not lost. The weekly numbers of hours of bright sunshine cover the seven days as they are taken from the daily records made at Rothamsted.

For the whole period of sixteen months the prevailing conditions of temperature and light, as indicated by the weekly means of maximum and minimum temperatures (Fig. 1), and the weekly hours of bright sunshine (Fig. 2), are summarised in the following table:

	Mean	Standard deviation
C. Mean maximum temperature	66.5° F.	11.7° F.
D. Mean minimum temperature	45.9° F.	4.66° F.
E. Hours of bright sunshine	20.3	16.6

The mean maximum temperature is naturally greatly influenced by the amount of sunshine, thus partly accounting for the large standard deviation. The minimum is much less variable, as during the winter months special care was taken to keep the night temperatures at a reasonably high level by means of artificial heating.

There is a close correlation between these three environmental conditions. The effect of each on the others depends upon the individual characteristics of the house, such as aspect and ventilation and artificial heating, and the extent of these effects can be measured by the correlation, as follows:

$$r_{CD} = +.6284 \pm .0384$$

$$r_{CE} = +.7560 \pm .0271$$

$$r_{DE} = +.2895 \pm .0595$$

¹ 1917. *Third Annual Report of Experimental and Research Station, Cheshunt, Herts*, p. 22.

The close association of hours of sunshine with maximum temperature is to be expected; nevertheless, taking into consideration that the mere total of weekly sunshine ignores its distribution between the several days of the week and the hours of its incidence on individual days, the

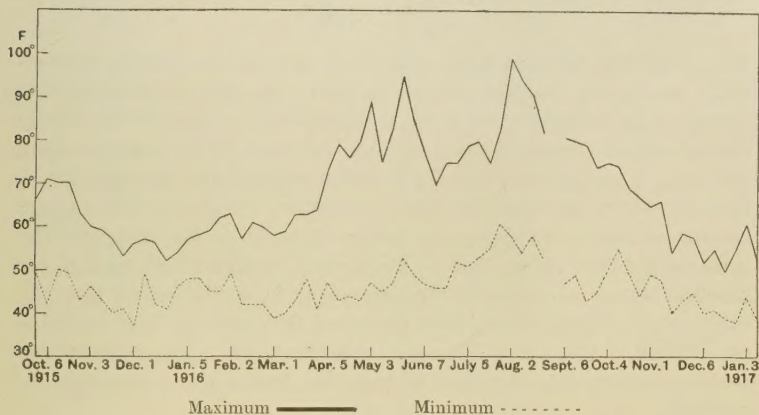


Fig. 1. Average weekly temperatures in roof water-culture house, Sept. 29th, 1915—Jan. 10th, 1917.

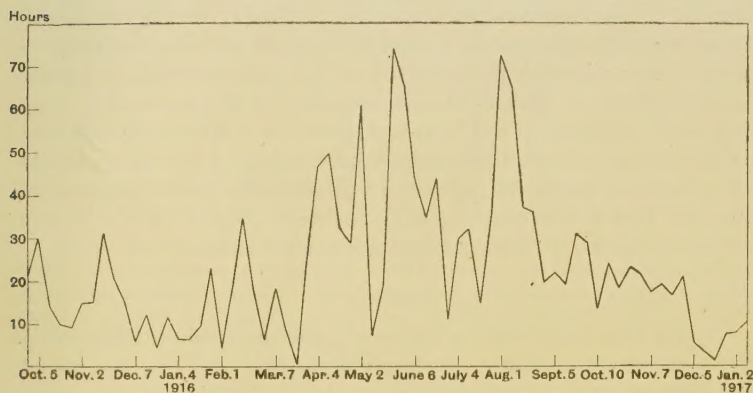


Fig. 2. Total hours of bright sunshine per week, Sept. 28th, 1915—Jan. 9th, 1917.

value obtained, .7560, is remarkably high. The correlation between mean maximum and mean minimum temperatures is also high, as is naturally the case; but the correlation between bright sunshine and mean minimum temperature would be higher, owing to the close association

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of both with the mean maximum, if some contrary tendency were not in operation. This is brought out by the partial correlations

$$E^r_{CD} = + \cdot 6534$$

$$D^r_{CE} = + \cdot 7709$$

$$C^r_{DE} = - \cdot 3638$$

The correlation between mean maximum and mean minimum for constant sunlight is $+ \cdot 6534$, slightly greater than before, showing that variations in sunlight affect these two variables in opposite directions; the correlation between mean maximum and sunlight for constant mean minimum is also greater, showing that the variations in mean minimum have tended to obscure this high correlation, a high mean minimum tending to occur with high mean maximum but with *low* sunlight. The third partial correlation, that between mean minimum and sunlight for constant mean maximum is strongly negative, and explains how the other two correlations have been obscured. The weeks of high sunshine are evidently the weeks of much radiation and night cooling; this partially counteracts the effect of high day temperatures produced by sunlight.

The small effect of sunshine on the range of mean minimum temperatures is brought out in Fig. 3, which shows that with considerable increase in total sunshine for a specified period (11 weeks) the highest mean minimum temperature is very little raised and the total range of weekly mean minima is little affected, at the same time that the highest mean maximum is pushed up many degrees and its total weekly range is greatly extended. It will be shown later that this relatively constant range of mean minimum temperature over prolonged periods is of great importance to the healthy growth of plants under these conditions of life, and that a comparatively slight increase above a certain level is very detrimental, but fortunately does not often occur.

METHOD.

It was necessary to select a species of plant for experiment that would grow under water culture conditions throughout the year and would not show too great a variation in the growth of individuals of the same age from a single sowing. Several years experience had shown that barley and peas are among the most satisfactory subjects for treatment by this method. In many respects barley is the better of the two, as if a pure line is used and the seeds are graded, very even growth can be obtained. Unfortunately during the winter months, in the "dead"

season of the year, it is often impossible to get satisfactory germination of barley, as root development is usually inhibited, and even if seedlings are obtained the young plants make very little growth. Consequently

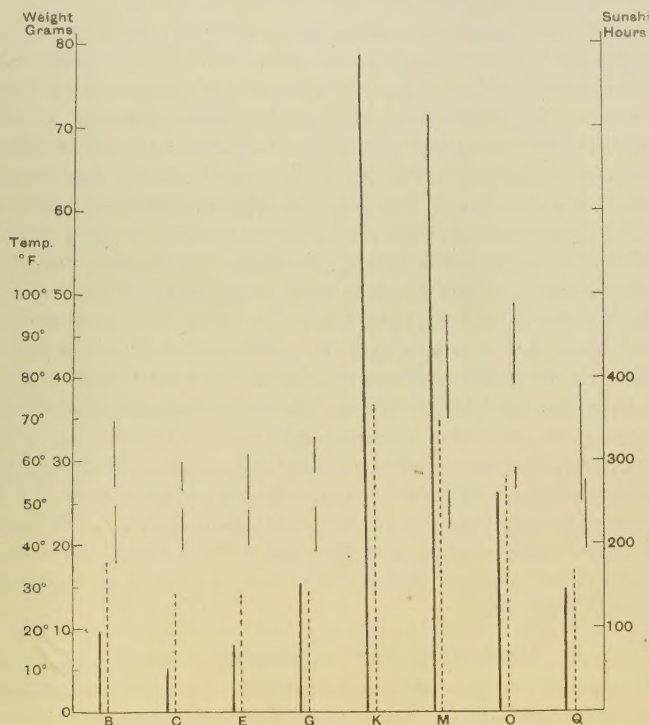


Fig. 3. Graph showing relations between total growth, total hours of sunshine and the range of mean maximum and minimum temperatures for several series of pea plants grown in water culture at different times of the year. All series were grown for 11 weeks except O, in which the plants died prematurely at the end of seven weeks.

Nutrient solutions changed weekly.

Heavy line = total growth.

Dotted line = total hours of sunshine.

Upper light line = range of maximum temperatures.

Lower light line = range of minimum temperatures.

peas were selected, for although the individuality of the plants is rather more marked, seedlings can be obtained throughout the winter, and a certain amount of growth can be relied on at whatever time the experi-

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ments are started. A dwarf variety, "Sutton's Harbinger," were used for the majority of the tests, but as unfortunately the stock ran out and could not be replaced the last four tests had to be carried out with Sutton's "King of the Dwarfs".¹

The seeds were graded and ranged between $\cdot 25$ – $\cdot 3$ gms. or $\cdot 3$ – $\cdot 35$ gms. for "Harbinger," and $\cdot 3$ – $\cdot 35$ gms. or $\cdot 35$ – $\cdot 4$ gms. for "King of the Dwarfs," only one range of weights being used in each test. At intervals of a few weeks sets of 160 pea seedlings were put into water cultures. Usually two parallel tests were carried out, in one of which the nutrient solution² was changed weekly and in the other the original solution was retained throughout the experiment. The same day that the water cultures were set up ten extra seedlings were prepared for drying, in order to obtain the initial dry weight of the plants. In addition 10 seeds of the grade used were weighed, to give the relation between seed and seedling after germination. At regular weekly intervals 10 plants from each set were removed from their solutions and the roots carefully washed two or three times in clean water to remove adherent food salts. The roots and shoots were separated before drying, and when the plants were in the fruiting stage the pods were removed, and dried and weighed separately. The 10 plants taken each week were selected at random from the whole group, and may be considered to represent more or less accurately the average growth of any similar number of plants at the time. The figures thus obtained were graphed, and the data yield valuable information as to the rate of growth of the pea plant and its relation to certain environmental conditions.

A. NUTRIENT SOLUTIONS CHANGED WEEKLY

The constant change of the nutrient solution ensured that a plentiful supply of food was always available and that starvation effects did not manifest themselves. The supply of water was maintained by replacing that which was lost from the bottles by transpiration from the leaves, and as the tests were carried out in the greenhouse the plants were not

¹ Our thanks are due to Mr Martin Sutton for the gift of all the seeds used throughout these experiments.

² Nutrient solution:

Potassium nitrate	...	...	1	gm.
Magnesium sulphate	...	...	$\cdot 5$	"
Calcium sulphate	...	...	$\cdot 5$	"
Sodium chloride	...	...	$\cdot 5$	"
Potassium di-hydrogen phosphate	...	...	$\cdot 5$	"
Ferric chloride	...	...	$\cdot 04$	"
Distilled water to make up 1 litre.				

subjected to rain or wind. Under these conditions the chief variable factors influencing growth were probably

- (1) temperature (maximum and minimum),
- (2) bright sunshine and light intensity,
- (3) humidity of the air.

Of these factors temperature records are available throughout. The sunshine figures give a very incomplete idea of the amount of available light or of the intensity of light but unfortunately no apparatus for automatically recording the changes in actual light intensity was available, and this part of the investigation is therefore incomplete. The humidity was not measured as at the time the possible significance of change in this respect was not realised, but readings taken during 1919 show that the range of humidity within the house is considerable. The results of the investigation are therefore chiefly of use in indicating the relationship of temperature and sunshine to the rate of growth at different periods of the life of the plant.

Eight series of peas were grown during these observations, the seedlings being placed in water cultures on the following dates:

"Harbinger."

Series B.	September 28th, 1915.	Series G.	January 4th, 1916.
C.	October 28th, 1915.	K.	March 10th, 1916.
E.	December 2nd, 1915.	M.	April 26th, 1916.

"King of the Dwarfs."

O.	July 3rd, 1916.	Q.	October 3rd, 1916.
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When seeds are germinated a loss in dry weight occurs owing to the fact that respiration goes on steadily from the beginning of growth, with a consequent loss of material by oxidation that at this stage is not balanced by the manufacture of fresh plant material. After the seedlings are set up in water culture this loss continues, for the same reason, over a period which varies in length according to the time of year (Figs. 4 and 5). Assimilation, which results in the building up of new substances from the air and the absorbed food salts cannot begin till the green leaves have appeared, and even then some little time elapses before the gain from assimilation balances the loss from respiration. Furthermore, the weights obtained show that the gain is at first very slow, as the leaf surface is initially small, and it is often several weeks before the young plant is again as heavy as the seedling was when first put into the culture solution. For the sake of convenience growth is divided into two periods which will be considered separately.

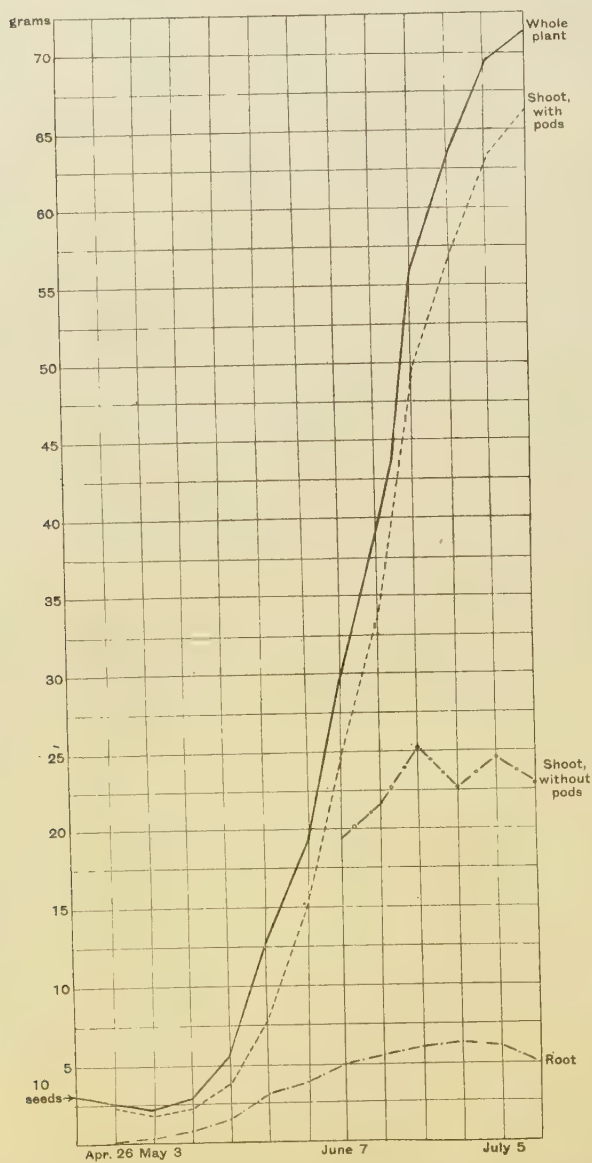


Fig. 4. *Summer Growth.* Dry weights of 10 pea plants, series M, grown from April 26th—July 12th, 1916. Nutrient solutions changed weekly.

(1) *1st period* from the seedling stage till the time that the plant regains its initial weight after the loss by respiration—*i.e.* the time during which a casual observer would say that the plant “makes no growth.”

(2) *2nd period*, succeeding the former, during most of which the plant is obviously making growth, and which continues to the end of the experiment.

1st period of growth.

In the division of the plant into root and shoot the remains of the seed are associated with the shoot. From the very first the root increases steadily, though slowly, in weight even while the total weight of the plant is diminishing. This increased root substance is therefore obtained at first at the expense of the shoot and must consist of material transferred from the seed or of the earlier products of assimilation or possibly

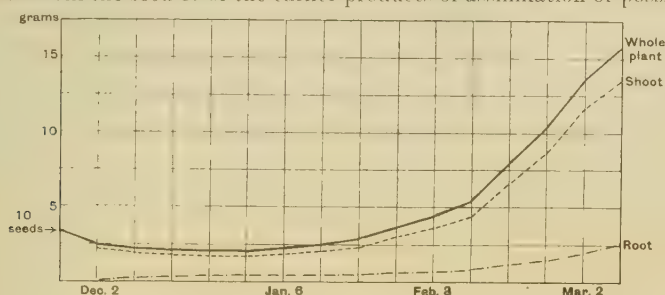


Fig. 5. *Winter Growth.* Dry weights of 10 pea plants, series E, grown from Dec. 2nd, 1915—March 9th, 1916. Nutrient solutions changed weekly.

of both. As the root thus increases in weight all the time, the loss of weight in the whole plant is less marked than in the shoot alone, and it therefore happens that the whole plant regains the initial seedling weight earlier than the shoot does. The length of time taken by the shoot to pass through the first period of growth varied with the time of year according to the prevailing temperatures as follows:

		Length of first period		
Experiment started:		for shoot	Max. weekly temp. ° F.	Min. weekly temp. ° F.
B.	Sept. 28th, 1915	3 weeks	70, 69, 70	42, 50, 49
C.	Oct. 28th, 1915	6 ,,	59, 60, 56, 54, 56, 58	46, 43, 40, 41, 37, 49
E.	Dec. 2nd, 1915	7 ,,	58, 55, 53, 56, 58, 59, 59	49, 42, 41, 46, 48, 48, 45
G.	Jan. 4th, 1916	4 ,,	58, 58, 62, 64	48, 45, 45, 49
K.	March 10th, 1916	3 ,,	64, 62, 66	43, 48, 41
M.	April 26th, 1916	2 ,,	89, 75	47, 45
O.	July 3rd, 1916	1 ,,	81	53
Q.	Oct. 3rd, 1916	2 ,,	74, 70	55, 49

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If these figures are appropriately grouped it is seen that the length of the first period bears a direct relationship to the range of the mean weekly maximum temperatures, the time decreasing with the rise of the mean maxima. On the other hand the range of the mean minimum temperature seems of little significance as the variations are very irregular and do not run parallel with the length of the first period of growth.

Length of period Weeks	Series	Range of Mean Max. temp.	Range of Mean Min. temp.
1	O	81 ° F.	53 ° F.
{ 2	M	{ 75-89	{ 45-47
{	Q	{ 70-74	{ 49-55
{ 3	B	{ 69-70	{ 42-50
{	K	{ 62-66	{ 41-48
4	G	58-64	45-49
6	C	54-60	37-49
7	E	53-59	41-49

It is thus evident that the rate at which assimilation is able to make good the loss by respiration increases directly with rise of temperature; at the lower temperatures a very small increase will reduce the period by a week or more, but higher up the scale a slowing off in the time reduction is noticed. It is probable that this is really a temperature effect rather than one due to light intensity, for with similar temperatures the same length of 1st period growth occurred at different times in the year, *e.g.* in series M started on April 26th the period of two weeks was the same as in series Q started on October 3rd, though the light intensity in the first case would probably be greater than in the second, while 68.2 hours of bright sunshine were recorded in the April period and only 42.1 hours in the October period.

The initial stage of growth, therefore, is represented by a period during which the weight lost by respiration is made up by a gain due to the beginning of assimilation, the rate at which this compensation occurs depending on the maximum temperature.

2nd period of growth.

All the series behaved in a similar way during the first period except with regard to the length of time that this persisted. The second period, that of active growth, is very different, and each series presents its own individual characteristics. Analysis of the results obtained, however, show that these characteristics bear a clear relation to the variable factors at work, and that the plant responds definitely and not arbitrarily to change in the environmental conditions.

(a) *Relation of total growth to sunshine and temperature.*

Under ordinary field conditions of cultivation the amount of water supplied as rain and the action of wind in drying out the soil and causing rapid alterations of temperature would influence the direct effect of temperature and sunlight. Under greenhouse conditions the first two factors are eliminated and the enquiry can therefore be narrowed down. In order to work out the relationship of total growth to sunshine and temperature it is essential that the growth should have occurred over equal periods, and for this reason only the first eleven weeks of each series are considered. One series, O, died after seven weeks, and this will be specially considered later on. The results are most clearly demonstrated by Fig. 3, in which are graphed for each series the total growth of the plant, the total number of hours of sunshine over the 11 week period, and the ranges of the mean weekly maximum and minimum temperatures over the same period. As would naturally be expected the total growth in summer was much in advance of that in winter. The three series C, E, G, started in October, December and January, show a steady increase in the total growth, G being more than twice as heavy as C. The available sunshine in all three cases was the same, but the range of maximum temperature was successively rather higher, though the greatest difference was only six degrees (60° – 66° F.). In the dead season of the year, therefore, slight differences in maximum temperature are very important in determining the amount of growth and they act independently of the available sunshine. The ranges of minimum temperatures were similar in all three cases and therefore did not influence the result.

The optimum time for growth under the experimental conditions was spring and early summer. In the presence of an abundant and unstinted food supply series K, started in March, made five times as much growth as G, started two months earlier. Double the amount of sunshine was available and the temperature ran up steadily from a rather low level until it almost reached the maximum weekly mean attained during the season. The series M, started a month later, did not do quite as well, but this may have been due to the fact that though the highest mean temperature was the same as K the means for the last three weeks were comparatively low.

A striking point emerged when an attempt was made to grow a series O at the beginning of July. The weather was bright and sunny throughout, the seedlings were started at 80° F., for only one week did

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the mean temperature fall as low as 75°, and for three weeks the average maximum was above 90° F. The plants were unable to stand the strain and after seven weeks growth they were dead, having made only 28 gms. dry matter compared with 39 gms. produced during a similar period in series M more than two months earlier. The mean minimum temperatures were comparatively high, the lowest mean being equal to the highest recorded at any other period. Evidently constant high temperature combined with excessive insolation under glass are inhibitory to growth, the best results being obtained with rather less sunshine and a greater range of temperature.

Autumn plants started in September and October resembled those grown in the winter, with a certain amount of extra growth due to a rather more generous supply of sun and heat.

It is thus seen that the possible amount of growth depends directly upon the sunshine and temperature at all periods of the year, but that beyond a certain point these beneficial factors become harmful and result in the premature death of the plants. Usually the two factors work together but when one factor, sunshine, remains constant, temperature is able to act independently in influencing growth. The converse of this may also be true but has not been demonstrated in these experiments.

(b) *Relation of the efficiency index to the time of year and the age of the plant.*

The "efficiency index" represents the rate per cent. at which fresh material is continuously added to the plant over a definite period¹, and it provides a very useful means of indicating the rate of growth at different periods of the life of a plant. In Fig. 6 the efficiency indices are plotted for weekly periods for all the series. As has already been stated during germination the seedlings lose weight by respiration, so that at the very beginning they weigh less than the seeds from which they came, and during the early part of the first growth period a further loss occurs until assimilation is in full play. At these stages the efficiency indices are negative, but when growth has fairly set in they are always positive, except occasionally at the very end after active growth has ceased but respiration is still continuing.

The curve shows at a glance that during the summer months, while growth is rapid, the efficiency indices reach a high level; in the spring and autumn they are medium, whereas in the depth of the winter they are very low and indicate that little more growth is made than will provide material to keep the plant alive and progressing very slowly.

¹ Blackman, V. H. (1919). "Compound Interest Law." *Ann. Bot.* xxxiii, pp. 353-360.

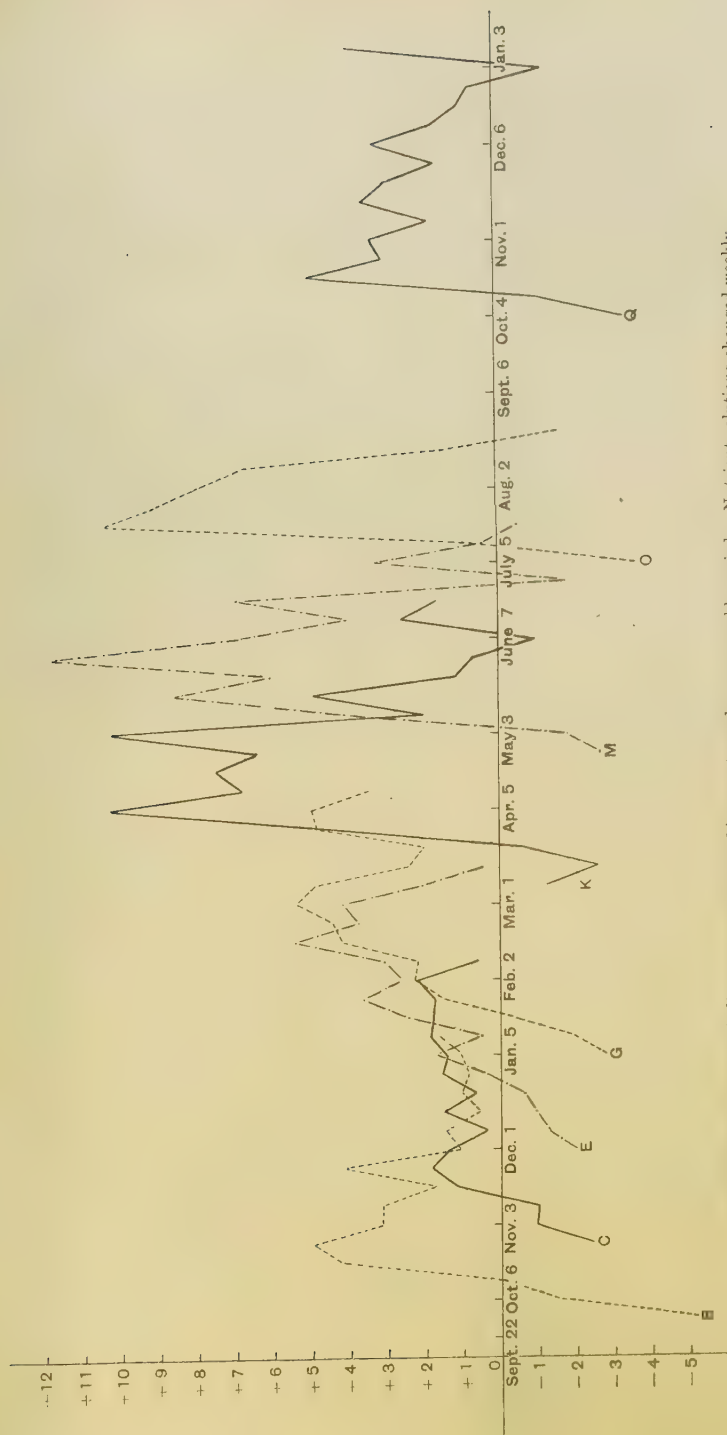


Fig. 6. Mean efficiency indices (per cent. rate of increase) per day over weekly periods. Nutrient solutions changed weekly.

Low efficiency indices were the rule from September to April¹, nearly all being below 5. During this period practically all the maximum temperatures were below 65° F. (see Fig. 1) and although the sunshine curve was much less regular than that of temperature all the weekly sunshine totals were below 35 hours, seven being below 7½ hours (see Fig. 2). During December the efficiency indices were very low and only varied within small limits, being much the same in series of different ages, which is not usually the case. This is evidently connected with the fact that during December occurred the lowest group of maximum temperatures for the whole year, and the period also embraced the largest group of low sunshine records. A rise in the indices began in January coinciding with an improvement in both temperature and sunshine. From March to August² high efficiency indices, much over 5, were obtained. Throughout this period the maximum temperatures were above 65° F. except during the first four weeks when they were slightly lower. Fifty per cent. of the weekly sunshine totals exceeded 35 hours, the excess often being considerable, six totals being 50 or more hours, while none ran below 7½ hours as happened earlier in the year. Thus broadly speaking high efficiency indices are associated with high temperatures and plenty of sun, while low indices occur in cold weather with deficient light.

Within this generalisation, however, more detailed information can be worked out.

An examination of the curves (Fig. 6) shows that during the greater part of the year, from March to November, the efficiency indices rise to their maximum very early in the life of the plant, usually within one or two weeks from the close of the first period of growth. In spring and autumn this maximum efficiency index is not very great, in summer it is much larger, but, given a moderate or plentiful supply of heat and sunshine, the impulse of the plant is to attain its maximum rate of growth as early in life as possible. This, of course, tends to the production of larger plants, as rapid growth at the beginning provides a large leaf surface at an early date so that more assimilation and increase of material can take place. When plants are started in the winter, in December or January, this rapid rise to the maximum does not occur, but the efficiency indices slowly climb up, taking about five weeks from the end of the first growth period to attain their maximum. This is associated with low maximum temperatures and low sunshine totals extending over the whole life of

¹ First series started in September, last series ended in April.

² First series started in March, last series ended in August.

the plant, so that at no time is the growth encouraged by a spell of greater heat or more abundant sunshine. As soon as the rate of growth reaches its maximum in the spring and autumn it begins to fall off slowly and irregularly but as at these times of the year growth was not completed within the period of experiment it is not certain what the behaviour would be at the end of growth. In the summer the rate of growth tends to fall away from the maximum but remains very high for several weeks. During this period the plants probably reach their maximum efficiency, making the fullest use of the food supplied under favourable conditions of temperature and sunshine. Growth is so rapid that it draws to a close towards the end of the experimental period and this is indicated by a sudden drop in the efficiency index, which occasionally becomes negative at the very end, indicating the continuance of respiration after assimilation has ceased, possibly combined with some degree of desiccation. The maintenance of a high rate of growth for several weeks during the summer combined with a sudden later drop is in marked contrast to the slow steady fall in the earlier part of the year, and explains fully why the later sown plants are so much more weighty than the rest. The later fall in the indices is not determined by either temperature or sunshine, but is a characteristic feature in the physiology of the plant occurring towards the end of growth, but the degree in which the fall is marked does depend to some extent upon the environmental conditions, as it is more obvious when favourable circumstances have kept up a rapid rate of growth until late in the life of the plant. The importance of the rapid rise to the maximum rate of growth is well shown by series K and M, both grown in the summer months. M reached a considerably higher maximum efficiency index than K, but whereas in K the rate of growth was at its maximum within a week of the 1st period, in M three weeks elapsed before this point was reached. Consequently, in spite of the ultimate rate being higher in M, the total growth was only 71 gms. against 91 gms. in K.

In the July series O the effect of the excessive heat and insolation was not manifest at first, as the maximum rate of growth was reached at the usual time, one week after the end of the first period. The rate fell off steadily though not abnormally quickly for another three weeks, but by that time the energy of the plants was exhausted and during the next fortnight the efficiency index fell rapidly until at the end the plants were prematurely dead.

An examination of the data by statistical methods shows a remarkable agreement with the results deduced by observation during growth and comparisons of the figures and curves for the individual series.

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Of the factors which affect the relative rate of increase of growth age, maximum and minimum temperatures and hours of sunshine can be investigated from the available data. The relation between age and rate of increase over the whole life is far from linear, so that the simple formulae of partial correlation cannot be applied, but the series of mean relative rates of increase may be divided into two satisfactorily linear series by separating the young plants (mean age up to four weeks old) from the old plants (mean age over four weeks). During the first period the mean efficiency indices rise to a maximum and during the second they fall from the maximum. This result bears out the observations that growth is divided into two distinct periods and that the tendency is for the maximum rate of growth to be attained at the beginning of the second period and to fall off afterwards.

When allowance is thus made for age the effect of environment upon the young and old plants must be considered separately.

The actual correlations between relative rates of increase (efficiency index) and the four other variates, age and the three environmental measurements, are

	Young plants	Old plants
Age	+·6995 ±·063	-·3498 ±·065
Mean maximum temperature	+·4444 ±·097	+·3907 ±·063
Mean minimum temperature	+·3958 ±·104	-·0588 ±·074
Bright sunshine	-·0132 ±·123	+·5177 ±·056

The quantities measure the extent to which the variables concerned are actually associated; growth in young plants is thus associated with relatively warm days and nights but not significantly with sunshine, in the older plants it is associated strongly with sunshine and warm days but not significantly with the night temperatures.

The combined effect of the independent variation of these four quantities may be expressed by regression formulae, the coefficients of which can be calculated from the correlations. If A stand for the age measured from a mean value of 2·5 weeks and 10 weeks for young and old plants respectively, C the mean maximum temperature measured from 67° F., D the mean minimum temperature measured from 46° F. and E the hours of bright sunshine in excess of 21 per week, then the relative rate of increase of young plants has the regression formula

$$\cdot 03 + 1\cdot 9544A + \cdot 3586C - \cdot 0190D - \cdot 1551E,$$

while for the old plants it is

$$2\cdot 91 - 2\cdot 121A + \cdot 07515C - \cdot 2320D + \cdot 0619E.$$

In interpreting these formulae it should be remembered that as C , D and E are closely associated the alteration of any one of them without the other is to some extent an unnatural process. Thus the fact that in both formulae the coefficient of D is negative, in the first to an insignificant extent but in the second significantly, shows that the greater growth has in general been made with the lower night temperatures *after allowance has been made* for the cooler days and less sunshine which are in fact associated with cooler nights. In the same way sunshine is detrimental to the seedlings *after allowance has been made* for its beneficial effect upon the day temperatures. Once the average effect of the environmental conditions is ascertained it is possible to obtain a truer representation of the relative rate of growth at different ages. For this purpose the average of the relative rates of increase for any age is corrected by means of the regression formula to its probable value under standard environmental conditions. The result of so doing is shown by comparing Figs. 7 and 8. The falling off of growth with age is more gradual after allowance has been made for changing environment; the points lie closer to the regression line for the older series, but the four first series are distinctly less linear. The whole series so corrected is likely to give a much truer picture of the normal history of the plant than when no correction is made. On the other hand, it is clear that irregularities are still present though they are smaller, and the three measures which have been used evidently do not give a complete picture of the plant's environmental experience during the week to which they refer. Among the other factors of environment that cause these irregularities are probably the distribution of the hours of sunshine over the day and week, the variation in the actual intensity of light apart from bright sunshine and the humidity of the surrounding air.

The abrupt rise in the relative rate of increase for the mean 9th period may possibly be mere coincidence but is more likely to have a physiological significance. Examination of the actual curves of efficiency indices show that somewhere in the neighbourhood of this period a real or secondary maximum efficiency index occurs, and in several cases the data show that just at this time the plants were in their first flush of flowering. This rise may therefore be real and connected with the initiation of sexual reproduction. If this be so it affords an interesting parallel to the increase in growth occurring at the time of puberty in human beings¹.

¹ Hall, G. S. (1908). *Adolescence*, Vol. I, pp. 59, 84, 93, 99.

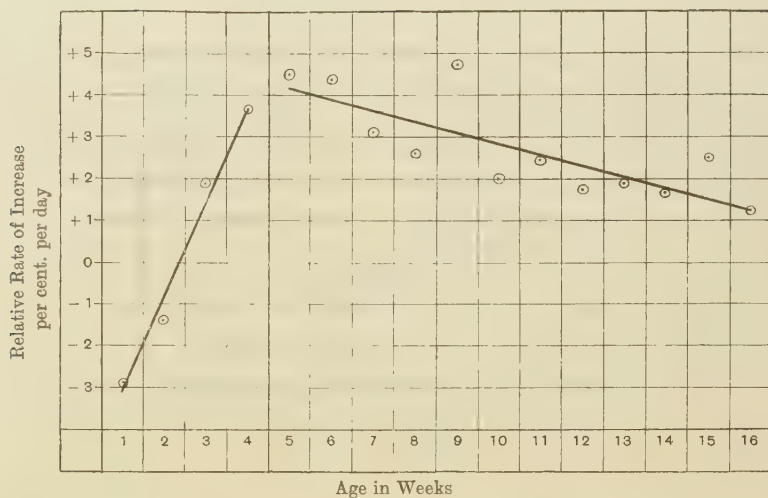


Fig. 7. Mean relative rate of increase at each age, with regression lines for young and old plants.

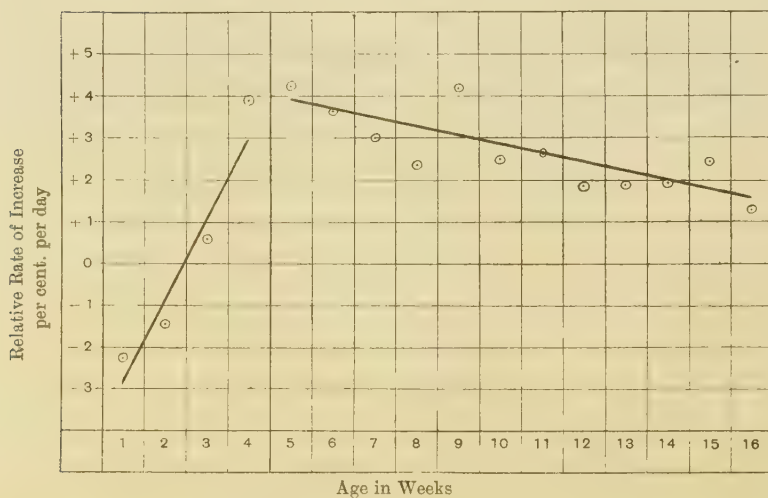


Fig. 8. Mean relative rate of increase at each age reduced to standard conditions, with regression lines for young and old plants.

{ Mean Maximum Temperature—67° F.
 { Mean Minimum Temperature—46° F.
 { Bright Sunshine—21 hours.

B. NUTRIENT SOLUTIONS NEVER CHANGED.

1st period of growth.

The series in which the solutions were never changed were set up to correspond in time as closely as possible with those in which the food was renewed. The following table shows how exactly the two sets correspond with regard to the length of the first period of growth.

Solutions never changed			Solutions changed		
Series started		Length of first period of growth for shoot Weeks	Series started		Length of first period of growth for shoot Weeks
A	Sept. 23rd, 1915	2	B	Sept. 28th, 1915	3
D	Oct. 29th	6	C	Oct. 28th	6
F	Dec. 4th	7	E	Dec. 2nd	7
H	Jan. 5th, 1916	4	G	Jan. 4th, 1916	4
I	Feb. 19th	4	No corresponding set		
L	March 10th	3	K	March 10th	3
N	April 26th	2	M	April 26th	2
P	July 3rd	1	O	July 3rd	1
R	Oct. 3rd	2	Q	Oct. 3rd	2

The only instance in which the first period varied by even a week was when there was five days difference in the date of beginning the experiment. At that time of year, in September, both temperature and sunlight were falling and the difference of nearly a week would fully account for the prolongation of the first period of growth in the later started plants. This series is therefore left out of consideration in drawing up comparisons. The close correspondence shows that during the first period of the plant's development under the experimental conditions the presence of an excess of nutrients, below toxic limits, has no effect upon growth. Very little mineral matter is sufficient to supply the needs of the seedling and the fresh quantity given when the solutions are changed is disregarded and exercises neither a beneficial nor harmful action. As a matter of fact, so little food salt is withdrawn from the solution at this time that the fresh solution added weekly closely resembles the old, and it is probable that no difference is detected by the plant.

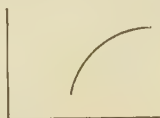
2nd period of growth.

As the series with changed and unchanged food solutions were carried on together the conditions of sunlight and temperature were identical in each case, the only different factor being that in one set an unlimited supply of food was available and in the other a very limited quantity was at the disposal of the plants.

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(a) Effect of restricted food supply on total growth.

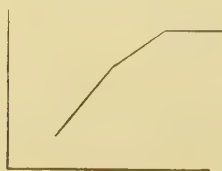
It was to be expected that the unchanged set would make less growth than the others, but the comparative relations of the amount of growth at different periods of the life of the plant are not altogether what were anticipated. As the plant grows and steadily draws on the limited food supply, the available amount of nutrient in the solution correspondingly decreases, and it might have been expected that with this decrease in available food a gradual decrease in growth would occur, giving a curve of the form



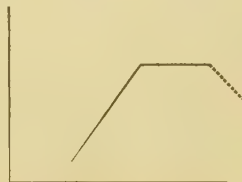
This, however, did not occur in any case. At all seasons of the year the growth in the earlier part of the second period showed a steady rise. In winter when growth was very slow the rise continued throughout the experiment; as the temperature and sunshine increased the time got shorter until eventually the rise reached its maximum in about three weeks. Then, quite abruptly, the growth changed and the curve flattened to a greater or less degree, but when once the change had occurred steady increase was again made, so that in most cases the curve took the form



In the early summer months growth ceased before the end of the experiment, causing a second flattening in the curve, whereas in the height of the summer no further growth was made after the first rise and a later drop often took place on account of loss due to respiration and desiccation.



Early summer.



Height of summer.

It is difficult to suggest an explanation as to why the abrupt changes followed by a period of steady growth should be the rule, instead of a gradual decrease in growth parallel with the gradual decrease in food. A comparison of these series (Figs. 9 and 10), with the corresponding sets with unlimited food supply (Figs. 4 and 5), shows that except during

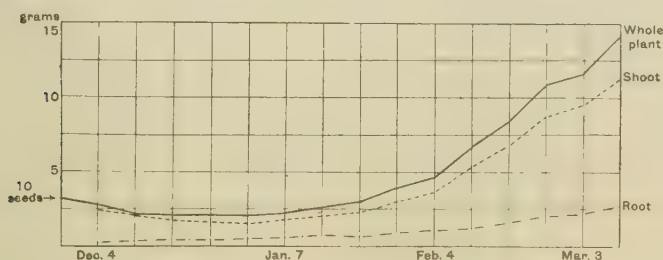


Fig. 9. *Winter Growth.* Dry weights of 10 pea plants, series F, grown from Dec. 4th, 1915—March 10th, 1916. Nutrient solutions never changed.

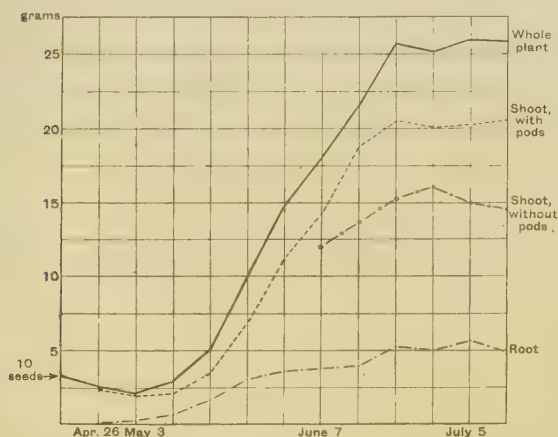


Fig. 10. *Summer Growth.* Dry weight of 10 pea plants, series N, grown from April 26th—July 12th, 1916. Nutrient solutions never changed.

the summer period of very rapid growth the amount of dry matter produced with limited and unlimited food supply is much the same or even identical for several weeks after the end of the first period, showing that the gradual reduction in food material does not always immediately affect growth. Eventually the well-supplied plants continue their steady

increase but the restricted ones fall off in the manner indicated above. In the summer with optimum conditions the extra food supply is beneficial from the first as the plants have a very high efficiency index and are able to utilise the nutrients to much better advantage, but though the restricted plants cannot keep pace with the others they rise in weight quite steadily for several weeks before depression sets in. It is only in series grown inclusively from March to June that the changed series pull ahead immediately the first period closes, while during the rest of the year the plants either do not begin to take advantage of the full supply in the one case or else they do not feel the lack of the full supply in the other till a later date.

The maximum amount of growth that can be made with a given constant supply of nutrients before growth ceases varies with the time of year, *i.e.* with the environmental conditions. Plants grown during May and June averaged 26 gms. dry matter and the total ranged down to 14 or 15 gms. in plants grown in spring or autumn. The winter grown plants did not reach the stage of ceasing to grow, but judging by the trend of the efficiency index curve it is probable that the dry weight would have been below that of the spring and autumn plants. The reason for this variation in dry matter produced is probably that growth is not only dependent upon the mineral food supplied to the root but also on the quantity of carbohydrates produced by assimilation. Under favourable conditions of temperature and sunlight when assimilation is greatly encouraged the formation of carbohydrate is very rapid and the amount of other constituents of dry matter become proportionately though not actually less. This is illustrated in an exaggerated form by those plants which store up starch or sugar, as potato and beet, but it holds good in other green plants as well. When conditions are less favourable to assimilation less carbohydrate is produced in proportion to the amount of food material absorbed, and with a limited supply of the latter a lower total growth is produced.

One curious discrepancy between the changed and unchanged series is noticeable. The maximum growth with unlimited food supply was made in a series grown from March to May, but in another grown from May to July there was a decided falling off which was attributed to less favourable environmental conditions. With limited food, however, the maximum growth was made in the second set, from May to July, so that apparently the environmental conditions that are optimum for dry weight production in the presence of plenty of food are not necessarily the optimum when a restricted supply is available.

Dry Weight per plant in grams.

	Unlimited food supply	Restricted food supply
March—May	K. 9.2	L. 1.85
May—July	M. 7.2	N. 2.6

(b) Effect of restricted food supply on efficiency indices.

The general form of the curves (Fig. 11) of the efficiency indices for the various series throughout the year is much the same whether the food supply is abundant or restricted, showing that on the whole there is a similar response to the environmental conditions that are common to both sets. In detail the correspondence is less close, indicating the influence exerted by the variable factor of food. In most cases during the earlier weeks the rates of growth go up or down together in both cases, as at this stage the environmental conditions of temperature and light common to both are more potent than the variation in food supply. Later on, when food begins to be much restricted in the one set, the efficiency index curves no longer run together, and they become much more irregular and erratic in the starved series. Under the conditions of restricted food supply, therefore, changes in the common environmental conditions produce exaggerated effects on the rate of growth. The foregoing applies more particularly to the spring and autumn months, but matters are rather different during the period of most rapid growth in the summer. At this time the conditions of light and heat are so favourable to growth that the plants can take advantage of a very large supply of food, and any restriction in this respect is felt more severely than when growth conditions are less good. Both sets of plants make the most of the available food immediately the first period of growth is over, and rise almost at once to a maximum efficiency index. This greatly depletes the food store, and when no more is supplied the rate of growth cannot be kept up and a rapid fall occurs, in contrast to the prolonged period during which a high rate of growth is maintained in the presence of abundant nutrients. In some cases the restricted plants never attain such a high efficiency index as the unrestricted, and the fall in the rate is less sharp, but in others the maximum index is as high or even higher and then an exceedingly sharp fall occurs, on one occasion (set P) the drop being from 11 to zero in three weeks.

A statistical comparison of the figures relating to the "changed" and "unchanged" series bears out the results obtained from observation of the curves of total growth, but shows more clearly the course of events in the later part of the life of the plant. The mean differences between

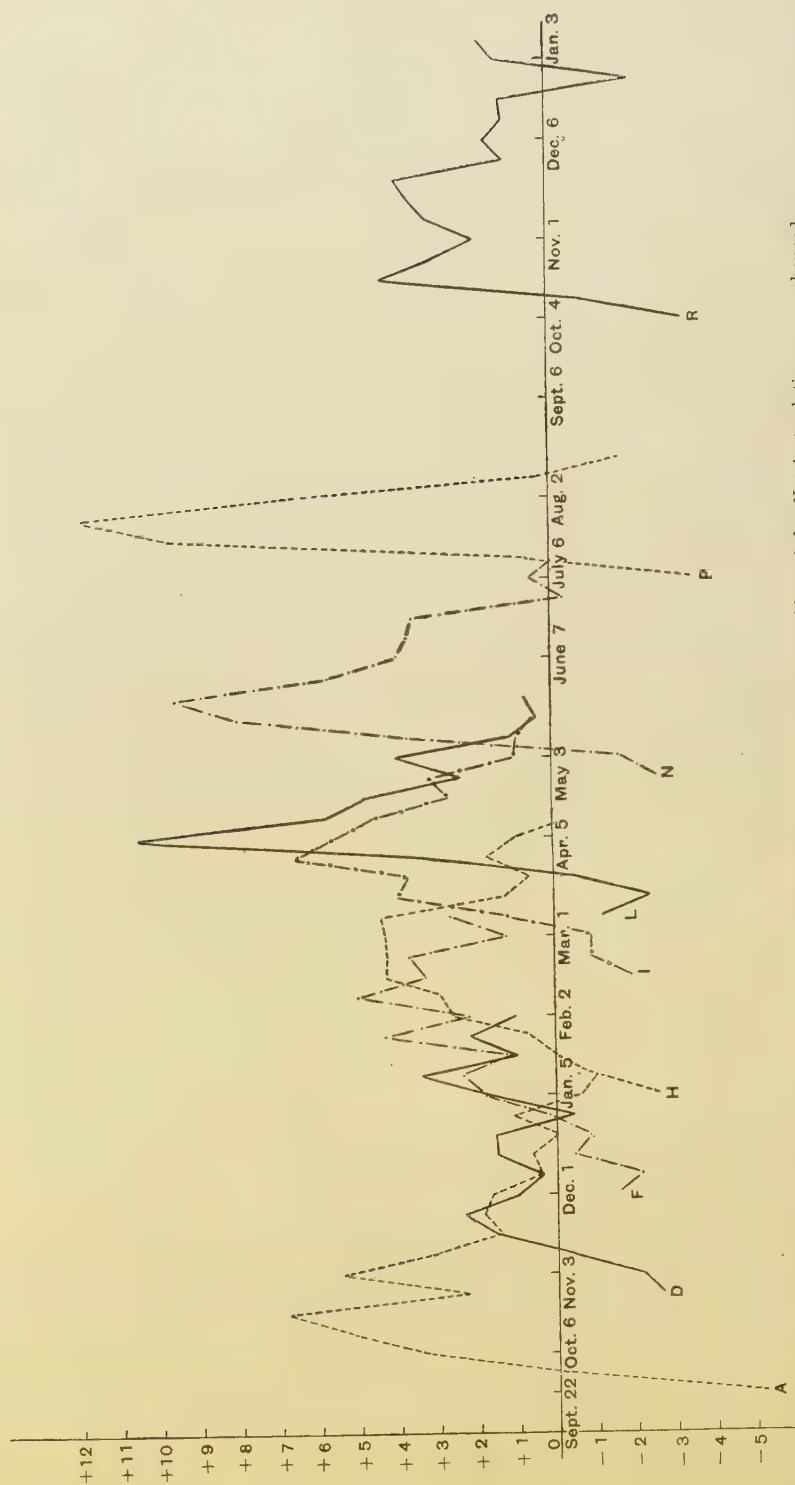


Fig. 11. Mean efficiency indices (per cent. rate of increase) per day over weekly periods. Nutrient solutions never changed.

the relative rates of increase (efficiency indices) week by week are shown in the following table, and are seen to fall into two distinct groups:

Week	Mean difference in efficiency indices of "changed" and "unchanged" series	
1	-	$\cdot 109 \pm \cdot 18$
2	+	$\cdot 110$
3	-	$\cdot 106$
4	-	$\cdot 062$
5	-	$\cdot 220$
6	+	$1\cdot 647$
7	+	$1\cdot 119$
8	+	$\cdot 993$
9	+	$1\cdot 768$
10	+	$\cdot 667$
11	+	$1\cdot 116$
12	+	$\cdot 455$
13	+	$1\cdot 700$
14	+	$\cdot 997$
15	+	$1\cdot 707$

- $\cdot 07 \pm \cdot 15$. Difference insignificant.

+ $1\cdot 19 \pm \cdot 20$. Difference definitely significant.

The insignificant differences obtained in the early weeks emphasize the fact that during the first period of growth and for perhaps a short time longer the plant gains no benefit from the constant renewal of the nutrient solutions, probably because during this time the demands on the external sources of nutrition are comparatively small, as some supply is still available in the seed and the manufacture of fresh food by assimilation is not yet in full swing. When once this period is over the variation in food supply makes itself felt at once, and this continues throughout the life-history. No constant change in the difference of the rate of increase is observable, but the variations are irregular throughout. This is somewhat contrary to expectation, as it was surmised that the drop in the efficiency indices in the unchanged series in late life would be far greater than that in the changed sets where no starvation effects were manifest. Apparently the natural fall in the indices that occurs late in life in all cases was more or less parallel to that induced in the semi-starved plants.

The correlations between relative rate of increase (efficiency index) and the three environmental measurements for the "unchanged" series are as follows:

	Young plants	Old plants
Mean maximum temperature ...	+ $\cdot 4760$	+ $\cdot 1695$
Mean minimum temperature ...	+ $\cdot 4170$	- $\cdot 0619$
Bright sunshine	+ $\cdot 0300$	+ $\cdot 4263$

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When these figures are compared with those for the "changed" series given on page 226, it is seen that with the young plants little difference occurs, showing that in early life the amount of food supplied in both sets was in excess of requirements and did not therefore act as a limiting factor. With older plants, however, when the food solutions were not renewed the correlation of rate of increase with mean maximum temperature was very much lowered and that with bright sunshine was also reduced to a significant extent. This indicates that when scarcity of food is acting as a limiting factor the plants are unable to take full advantage of the available bright sunshine, while at the same time the beneficial influence of high maximum temperature is reduced to an even greater degree.

Another interesting point can be elucidated from the comparison of seven pairs of changed and unchanged series, each pair being grown under identical conditions for the same length of time. The total variance¹ at any given age, for older plants (in the second period of growth), may be roughly analysed into

37 per cent. fortuitous variation (due to individual difference of seeds etc.).

38 per cent. known environmental factors.

25 per cent. unknown environmental causes (irregularities of temperature and light not affecting the means, humidity etc.).

The percentage of variance (38 per cent.) that can be attributed to the known environmental causes of maximum and minimum temperatures and total sunshine is remarkably high and indicates that these are the most potent of the factors acting upon growth. The causes of fortuitous variation are less clear, and the percentage (37 per cent.) seems rather high considering that it is a mean figure, as under the greenhouse conditions the extremes of individual variation in a number of plants generally reach about the same figure, and the mean variance in the rate of increase might be expected to be less. The extent of individual variation in weight, however, regarded as a percentage difference, must not be confused with the variance of the efficiency index which is to be ascribed to various groups of causes. Further work on this point will be necessary, for if it could be more fully explained it would give more reliable information than is at present available as to the influence of the individuality of plants upon the validity of experimental results.

¹ The mean square deviation of the rate of increase at given age is used as a measure of the variance, and the percentage figures are calculated from this.

GENERAL OBSERVATIONS ON GROWTH.

(1) *Comparison of root and shoot growth.*

Inspection of the growth curves shows that at all stages of growth and at all seasons the dry weight of the root is less than that of the shoot. As the plants get older the shoot becomes rapidly heavier under favourable conditions, but the increase in root weight is by no means parallel to that of the shoot as it is very much slower, with the result that when very heavy growth is ultimately made by any plant the discrepancy in the dry weight of the root and shoot is very marked. This change in the relations between the two parts of the plant is well shown by the ratio between the dry weights of shoot and root for the weekly periods for which figures are available (Figs. 12 and 13).

In the very young seedlings, at the stage at which they are put into the food solutions, only part of the material stored in the seed has been utilised and the roots are as yet very small. Since the seed is included with the shoot the shoot/root ratio at this time is very high, ranging from about 14–32 according to circumstances¹. From this time more normal relations establish themselves, for the seed store becomes rapidly depleted and the ratio is that between the actual shoot (stem and leaves) and the root. The shoot/root ratio continues to fall at a decreasing rate for a varying period, the lowest ratio corresponding fairly closely with the end of the first period of growth, though it may be reached a week or two earlier or later. From this time onwards, when there is no deficiency of food (Fig. 12), the shoot increases more rapidly than the root in weight, and the shoot/root ratio goes steadily up. The more rapid the growth, the more marked this rise, and in the summer months under optimum conditions of temperature and light the low proportion of root to shoot is most striking. When the food supply is limited (Fig. 13) and less growth is made the figures do not reach such a high level, but exactly the same course of events is noticed, as a rise in the shoot/root ratio occurs from about the end of the first growth period and the largest ratios are obtained in the summer months.

An explanation of this change in the proportion of shoot and root may be found in the different mechanical construction of the two parts. The two main functions of the root are the absorption of water containing dissolved food substances and the fixing of the plant in the substratum. For the efficient performance of the first function a large area

¹ For economy of space this initial high ratio is omitted from Figs. 12 and 13, the first ratio on the curve being that obtained after one week's growth in nutrient solution.

capable of constant renewal is desirable in order that the maximum proportion of root hairs, the actual absorbing organs, may be provided and renewed as they die off. The root, with its multiplicity of long slender

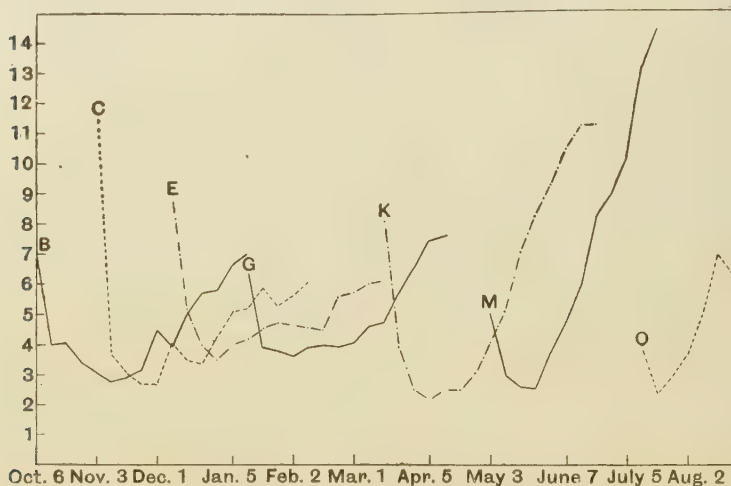


Fig. 12. Shoot/Root Ratios for weekly periods. Oct. 6th, 1915—Aug. 23rd, 1916.

Nutrient solutions changed weekly.

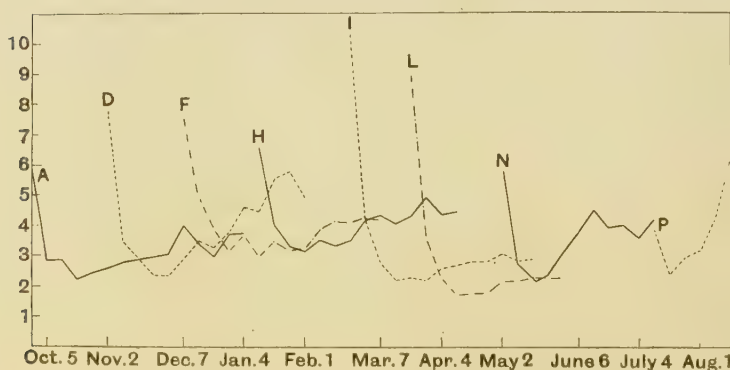


Fig. 13. Shoot/Root Ratios for weekly periods. Sept. 28th, 1915—Aug. 15th, 1916.

Nutrient solutions never changed.

branches continually growing in length, fulfils this condition admirably and each addition of an extra rootlet provides an additional absorbing surface out of all proportion to the quantity of plant material used up in

the production of the rootlet. In this way a great increase in absorption can be provided for with comparatively little increase in the dry weight of the root. The same structure is also the most economical for the performance of the second function of fixation, as the multitude of fine strands result in a very effective supporting agent. The shoot, on the other hand, is chiefly concerned with the processes of respiration, transpiration and assimilation. For these a considerable bulk of tissue is desirable in order to provide an adequate supply of intercellular spaces, chlorophyll and storage tissue and also that a broad surface may be presented to make the most effective use of sunlight in the elaboration of food material. In order to carry a great expanse of leaf stout stems are necessary, and consequently a large amount of material has to be used in the construction of the shoot. As the plant gets older, the root is increasing its absorbing capacity at the expense of comparatively little new material while the shoot is using up a great deal for growth and may also be acting as a storehouse of reserves, so the relative weights of the two parts tend to diverge more and more. The more rapid the growth, the more rapid the divergence, as is shown graphically by the large shoot/root ratio attained under optimum conditions.

The behaviour of root and shoot with regard to temperature is distinctly different. It has already been shown that during the first period of growth, whatever the season and the temperature, the weight of the shoot falls and then rises again, whereas the root increases steadily in weight from the beginning. After this period the temperature factor is very potent. The shoot weight at all seasons continues to rise, slowly with low mean maximum temperatures, rapidly with high mean maxima. Under no circumstances with the mean maxima attained in this experiment did the increase in dry weight of the shoot cease even for a time until the very end when growth was completed. Up to a certain limit, also, increase in the rate of shoot growth is correlated with rise of temperature. Root growth, on the other hand, is much affected by low mean maximum temperatures, and practically no advance was made in any series, irrespective of the food supply, from mid-November to January, over a period during which the mean maxima were consistently below 60° F. Rise in temperature does not have the same relative beneficial action on the root that it does on the shoot, as no sharp rises in root weight could be detected when temperatures went up. There is some indication that whereas the roots can grow satisfactorily in high temperatures when they are subjected to plenty of heat from an early period of life, root growth is severely checked or even stopped if a sudden and prolonged increase in temperature occurs when the plant

is well developed, but this check in root increase does not necessarily imply a corresponding check to the shoot.

Cessation of root increase is a constant phenomenon and always occurs some time before the shoot stops growing. In some cases there is evidence that an actual decrease in weight occurs after this period but as this is most marked in the plants which are grown in constantly changed food solution it is possible that the loss may be partly due to abrasion in the mechanical process of handling, the loss not being made good by growth. Without further information it is impossible to say whether this loss of weight in the roots is of real significance.

(2) *Shoot growth and pod formation.*

As the duration of the tests was limited to a certain number of weeks few of the series reached the stage of pod formation. Of these, three received abundant food and one was limited in this respect. As soon as pod formation begins the rate of growth of the stem and leaves, excluding the reproductive organs, falls off immediately and relatively little extra weight is put on, though the increase in weight of the whole shoot is exceedingly rapid (Figs. 4 and 10). Up to the time of flowering the energy of the plant is directed to building up a healthy body capable of bearing the strain of reproduction. When seed formation begins the energy is diverted into this channel, and the shoot (stem and leaves) becomes merely the agent whereby the necessary materials for building up the fruit and seed are supplied. Consequently it is now unnecessary for more food to be expended in the production of a bigger shoot, so little increase takes place and there is evidence that at a later stage still loss of weight occurs owing to the transference of the actual substance of the stem and leaves to the seed. This transference has been proved in the case of certain other plants, among which barley and wheat may be instanced¹. The most rapid increase in the weight of the pods occurs during the first two or three weeks after they appear, after which the increase slackens off till eventually a drop in weight may occur associated with the onset of maturation and desiccation.

(3) *Relation of nitrogen absorption to dry matter produced.*

A true estimate of the amount of nitrogen taken up can only be obtained by analysis of the plant itself, but labour difficulties during the war rendered it impossible to have the necessary analyses made. In

¹ (a) Brenchley, W. E. and Hall, A. D. (1909). "Development of the Grain of Wheat." *Journ. Agric. Sci.* III, pp. 195-217.

(b) Brenchley, W. E. (1912). "Development of the Grain of Barley." *Ann. Bot.* XXVI, pp. 913-928.

a few series, however, the water culture solutions were sampled at intervals and the nitrogen present estimated as potassium nitrate. These figures indicate the amount of KNO_3 that had disappeared from the solutions in a given time and enable some idea to be formed of the amount of nitrate taken up and utilised by the plant in the production of varying weights of dry matter. The great objection to this method of estimating the nitrogen absorption is that the amount of nitrogen that is lost by decomposition or denitrification is probably a variable unknown quantity for which it is difficult to devise a method of determination. Tests made at various times with solutions allowed to remain in the bottles for some days or weeks without any plants growing in them seem to show a slight loss of nitrate, though this is not very considerable even after the lapse of some time. The figures obtained in the present experiments are probably sufficiently accurate to give a true indication of the trend of affairs even though the actual quantitative measure they represent cannot be fully accepted.

Analyses of the solutions for KNO_3 were made at various times in the unchanged series L and N and the changed series K and M. When the solutions were unchanged the KNO_3 available throughout the life of the plant was only .6 gm. per plant and by the time the experiments were finished very little or none of this remained in the solutions. The results obtained in these cases are summarised in Table I, in which the figures apply to the unit of ten plants, grown in six litres of solution.

Table I (Solutions not changed).

Date	After — weeks growth	KNO_3 lost from 6 litres solution	Dry weights of 10 plants produced in period	Ratio of KNO_3 lost to dry matter produced over whole period
Series L				
April 21st	6	4.02	8.044	1 : 2.00
May 12th	9	5.76	14.887	1 : 2.59
May 19th	10	5.76	15.337	1 : 2.63
Series N				
May 10th	2	.96	0.359	1 : 0.37
May 17th	3	1.89	2.520	1 : 1.33
May 24th	4	3.16	7.292	1 : 2.31
June 23rd	8	5.92	23.166	1 : 3.91

The ratio column of Table I shows clearly that as the pea plant gets older the increase in dry matter produced becomes less dependent upon the amount of nitrate absorbed by the roots, and that even when very little intake is possible owing to exhaustion of the food supplies some

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growth can still occur by means of photosynthesis. It appears that early in life, before the high tide of assimilation is reached, the plant absorbs a relatively large amount of nutrient salts by means of the roots without producing a correspondingly large quantity of dry matter, but as time goes on increasing amounts of dry matter are formed for the same amount of absorbed nitrate. The more favourable the season for assimilation the greater the amount of dry matter ultimately produced per unit of KNO_3 , as is seen from the fact that for every gram of KNO_3 3.91 gms. of dry matter were produced in series N in the summer months against 2.63 gms. in series L in late spring.

In the changed series K and M a fresh supply of nitrate was added every week and the results give the measure of absorption and growth for weekly periods, instead of extending over the whole life of the plant to date as in the former case. Under these circumstances it is to be expected that greater irregularity will occur in the figures, as the constant changes in environmental conditions will only be averaged up for a week instead of for the whole time of growth. Even so, however, there is some indication, especially in series M (Table II), that as the plant gets older relatively less nitrate is utilised in the production of dry matter, though the evidence is less conclusive than where semi-starvation occurs.

These results bring out the fact of the relative greater importance of assimilation at the time of heavy growth, when more efficient use is made by the plant of the food material absorbed by the roots. For full information on this point it would be necessary to have a series of analyses of the plant and the nutrient solution at regular intervals in order that the various factors introduced by loss, absorption and assimilation might be examined and correlated.

Table II (Solutions changed).

Date	At end of — week	KNO_3 lost in the week from 6 litres solution	Dry weights of 10 plants produced in the week	Ratio of KNO_3 lost to dry matter produced in the week
Series K		grams	grams	
April 14th	5th	2.34	3.176	1 : 1.36
„ 21st	6th	1.65	5.738	1 : 3.48
May 12th	9th	3.72	6.650	1 : 1.79
„ 19th	10th	4.14	20.984	1 : 5.07
„ 26th	11th	3.52	5.847	1 : 1.66
Series M				
May 10th	2nd	1.29	.737	1 : 0.57
„ 17th	3rd	1.89	2.409	1 : 1.27
„ 24th	4th	2.46	2.792	1 : 1.14
June 23rd	8th	4.44	16.509	1 : 3.72

SUMMARY.

1. Growth may be divided conveniently into two well-marked periods.

(a) *1st period*, from the seedling stage till the time that the plant regains its initial weight after the loss by respiration, *i.e.* the time during which a casual observer would say the plant "makes no growth."

(b) *2nd period*, succeeding the former, during which the plant is obviously making growth, and which continues till the latter ceases and desiccation sets in.

2. The length of the first period varies inversely with the mean maximum temperature, as the rate at which assimilation is able to "make good" the loss by respiration increases directly with rise of temperature, up to a certain limit.

3. The possible amount of growth as measured by the dry matter produced depends directly upon the bright sunshine and temperature when the food supply is adequate, but when the latter is limited the total growth is much less owing to the lack of material for building up the tissues. Beyond a certain limit, however, the beneficial factors of heat and bright sunshine become harmful and result in the premature death of the plant.

4. During the first period the rate of growth as shown by the efficiency index was associated with relatively warm days and nights, bright sunshine having little significant effect; the light, however, was good throughout for the season of the year. During the second period the rate was associated strongly with sunshine and warm days, but not significantly with the night temperatures, which did not fall below 32° F.

5. During the greater part of the year the maximum rate of growth (highest efficiency index) is reached early in life, very soon after the second period begins. Under favourable environmental conditions a high rate of increase is then maintained for several weeks, but in less favourable circumstances the efficiency index rapidly falls. In winter, when temperatures run low and there is little bright sunshine, the maximum rate of growth is not reached till several weeks after the beginning of the second period, and even then the efficiency index is not very great.

6. Plants with a restricted food supply make less total growth than those with abundant food. The falling off in the amount of dry matter produced does not seem to be gradual but is marked by definite periods of which the incidence varies at different seasons.

7. Broadly speaking the response of plants to the environmental conditions is similar whether the food supply is abundant or restricted,

though the mean rate of growth is lower when food is scarce. During the first period the excess of food has no significant effect upon the rate of growth, but during the second period the mean differences in the rate of increase in the presence of abundance and of scarcity of food are strongly significant in favour of the well supplied plants.

8. During the early weeks, corresponding approximately to the first period of growth, the shoot/root ratio falls, owing to the steady increase in root weight which is associated at first with a decrease and later with an increase in shoot weight. During the second period of active growth the shoot increases in weight far more rapidly than the root, and thus the shoot/root ratio rises steadily. Increase in shoot growth is closely associated with rise in temperature, though the lowest mean maximum attained in the experiments did not cause a cessation of growth. Root growth is much affected by low mean maximum temperatures and practically ceased, under the experimental conditions, when they were consistently below 60° F. Rise in maximum temperature had much less beneficial action upon the roots than upon the shoots.

9. In early stages of growth the amount of nitrate absorbed by the plant is relatively large in comparison with the dry matter produced, but later on more dry matter is formed in proportion to the same amount of nitrate, owing to the accumulation of the products of assimilation.

In conclusion I wish to express my indebtedness to Mr R. A. Fisher, who has examined the figures and has furnished me with the statistical information embodied in this paper.

NOTE.

SOME FACTORS IN PLANT COMPETITION

(THIS JOURNAL, VOL. VI, NOS. 2 AND 3, 1919.)

By an oversight the weights of the barley and mustard seeds, used in the calculation of the efficiency indices, were omitted.

Mustard.	Tables I—II,	pp. 145—147.	Average wt. per seed	·007 gm.
Barley.	Tables III—VI,	pp. 149—150.	„ „	·055 „
Barley.	Tables IX—XVI,	pp. 162—167.	„ „	·065 „

In each case the efficiency indices are per cent. per day.

GLOMERELLA CINGULATA (STONEMAN) SPAULD.
AND V. SCH. AND ITS CONIDIAL FORMS, *GLÆO-
SPORIUM PIPERATUM* E. AND E. AND *COLLETO-
TRICHUM NIGRUM* E. AND HALS., ON CHILLIES
AND *CARICA PAPAYA*.

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(With Plate X.)

ON chillies or peppers (*Capsicum annuum* and *C. frutescens*) three anthracnoses have been recorded to date. In 1889, Ellis described a very destructive disease in America caused by *Glæosporium piperatum* E. and E. Halstead¹, in the following year, discovered another which was considered to be different from the previous one, on account of the presence of setae in the acervuli; it was consequently named *Colletotrichum nigrum* E. and Hals. In 1913, Sydow² described a new species of *Vermicularia* on chillies, sent to him by Mr McRae from South India. In India, especially in Bihar and Madras, *Vermicularia Capsici* Syd. is the most destructive disease and causes a great deal of damage to the fruits and to the plants as well, at least in Bihar. The other two diseases have not as yet been reported to do much damage in India, but in Burma they seem to cause much loss of the fruits. In 1917, an experimental plot of two acres on the Pusa Farm bore a crop of chillies. The damage done to the plants and fruits by *V. Capsici* was considerable but *G. piperatum* was rarely found on fruits and *C. nigrum* was much more scarce. However, on the stem *G. piperatum* was slightly more prevalent than on the fruits but it was invariably found only on the stem attacked by *Choanephora Cucurbitarum* (B. and Rav.) Thaxter and *V. Capsici*. As a rule only mature fruits are attacked by *G. piperatum* and the other two

¹ Halstead, B. D. *Report of the Botanical Department, New Jersey Agr. Col. Exp. Stat.*, 1890, pp. 358 and 359.

² Sydow, H. Beiträge zur kenntnis der Pilzflora des Südlichen Ostindiens-I. *Ann. Myc.*, xi, 1913, p. 329.

anthracnose fungi and they produce similar discolorations. The disease is first visible as a small circular black or greenish black spot, which is generally, but not always, slightly depressed. As the infection spreads the fruit loses its normal red colour and turns whitish yellow or greenish yellow, reddish yellow or straw coloured. It also becomes prematurely dry and very brittle. However, the acervuli of *G. piperatum* can be readily distinguished from those of the other two fungi by their pink colour, especially when fresh. *Colletotrichum* and *Vermicularia* acervuli are not easily distinguishable because of the black colour due to the presence of setae; but the *Vermicularia* acervuli generally look more bristly and more erumpent as a part of the stroma is above the epidermis. Old *Glaeosporium* acervuli, which have turned black, may be mistaken for *Colletotrichum* acervuli on superficial examination.

The disease due to *V. Capsici* will be treated in a separate paper, so a further account of it is unnecessary.

G. piperatum E. and E.

The diseased part of the fruit shows slightly raised points. This is due to the development of acervuli underneath them. With the growth of the acervuli the skin is ruptured by elliptical, triangular or irregular rifts. If the diseased spot be examined with a hand-lens, crater-like structures filled with beaded or cauliflower-like pink growths are visible due to the development of spore masses. The acervuli start from the centre of the diseased spot and are generally concentrically arranged but they may also be scattered. They are, when fresh, oily and flesh pink in colour which may either change to dull light pink when they become old or to black, from margin inwards.

In the epidermal and sub-epidermal cells hyphae collect together and eventually develop into a pseudo-parenchymatous stroma; from the top of which conidiophores arise. As a rule the latter are short and conical with a tapering apex but they become much elongated and narrow under extremely moist conditions. They measure $11.0-18.7 \times 2.7-4.9\mu$. From tips of the conidiophores spores are cut off. Under the pressure of the growth of conidiophores and development of spores the cuticle is pushed up and eventually ruptured. At first the raised cuticle keeps the conidia more or less confined underneath it and allows their escape only through a small opening but later the cuticle is completely thrown aside (Plate X, Fig. 2). It is the frayed edges of this ruptured cuticle that give the diseased part of the fruit, at times, a scaly appearance. The spores are held together in a gelatinous mass at the opening of the acervulus

as in other species of this genus. They are elliptical with broad round ends, hyaline in colour and have an oil globule in the centre (Fig. 3). They measure $11.0-21 \times 4.4-5.5\mu$.

This development of the acervulus of *G. piperatum* E. and E. is similar in all its details to that of *Colletotrichum Lindemuthianum* (Sacc. and Mag.) Br. and Cav. as described by Edgerton¹ except that in the former the stroma of pseudo-parenchymatous cells distinctly precedes the formation of conidiophores while in the latter the stroma is of a later origin.

Specimens of *Colletotrichum nigrum* E. and Hals. on chilli fruits collected in Burma and Pusa show that this fungus agrees in all characters with *G. piperatum* except that the acervuli of *C. nigrum* have long rigid dark brown setae up to 150μ long and 4μ broad.

The perfect stage of *G. piperatum* and *Colletotrichum nigrum* has not previously been recorded on the host plant but at Pusa it has been found on fruits on rare occasions. Miss Stoneman², who succeeded in growing in cultures the perithecial stage of *G. piperatum*, named it *Gnomoniopsis piperata* which was subsequently changed to *Glomerella piperata* (Stoneman) Spauld. and v. Sch.; and Taubenhaus³ considers, from inoculation experiments, *Gl. rufomaculans* (Berk.) Spauld. and v. Sch., which is the same as *Gl. cingulata* (Stoneman) Spauld. and v. Sch. according to Edgerton⁴, to be the perfect stage of *C. nigrum*. Butler⁵ is inclined to think *Gl. piperata* (Stoneman) Spauld. and v. Sch. is synonymous with *Gl. cingulata*. The author is of opinion, for reasons given below, that *G. piperatum* and *C. nigrum* are identical and that their perithecial stage is *Gl. cingulata* (Stoneman) Spauld. and v. Sch.

Growth of Gl. piperatum E. and E. in cultures.

Cultures on glucose-meat-extract-agar started from conidia give for the first few generations a fairly abundant aerial growth which to begin with is white but soon turns pink owing to the development of spores. In places, the culture turns black or greenish black on account of the formation of strands of dark brown hyphae, especially at the lower

¹ Edgerton, C. W. The Bean Anthracnose. *Louisiana Agric. Expt. Sta. Bull.*, 119, April, 1910, p. 5.

² Stoneman, B. A comparative Study of the Development of some Anthracnoses. *Bot. Gaz.*, xxvi, p. 104, 1898.

³ Taubenhaus, J. J. A further Study of some Gloeosporiums and their Relation to a Sweet Pea Disease. *Phytopathology*, II, No. 4, p. 159, 1912.

⁴ Edgerton, C. W. The Physiology and Development of some Anthracnoses. *Bot. Gaz.*, xlv, p. 401, 1908.

⁵ Butler, E. J. *Fungi and Disease in Plants*, p. 355, 1918.

end of the culture tube and at the margin of the agar medium. By continuous subculturing on agar media and on sterilized potato tubers and chilli pods the spore-bearing capacity is lost and the cultures remain sterile, and on glucose-meat-extract-agar the growth is no more aerial but matted and submerged. But if transfers from this sterile fungus are made on sterilized chilli or potato stems, the growth is again fertile; the conidia are borne on tips of hyphae and in pink acervuli; and in subcultures made on glucose-meat-extract-agar from this fertile culture the mycelium is aerial, bears conidia and the growth resembles that obtained originally from conidia planted on glucose-meat-extract-agar but after three or four generations on the same medium it again becomes sterile and confined to the substance of the medium.

The mycelium is generally composed of two kinds of hyphae, one very thin and the other very broad, closely septate and highly vacuolate. At times intercalary vesicles are formed in the hyphae. The hyphae, both broad and thin, often get fused together and form a network.

The conidia are developed either in acervuli, as in *Melanconiaceae* or on the tips of lateral branches of hyphae, as in *Hyphomycetes*. The acervulus in cultures originates as an aggregation of hyphae forming a stroma which from its commencement is brown like that of an acervulus on the host plant. From the stromatic cells hyaline basidia or conidiophores are developed from the tips of which conidia are produced in succession. The stroma is usually without appendages but at times it bears brown hyphae, generally flexuous, rarely rather stiff. These appendages have some remote resemblance to the setae of a *Colletotrichum* acervulus.

The spores, when sown in water, swell before germinating. At times only a part of the spore is swollen, the unswollen end having a pinched-in appearance. The germinating spore (Fig. 3) may become septate. The germ-tube is developed from either end or from both the ends. Appressoria are formed at the tips of the germ-tubes. The germ-tubes occasionally bear secondary conidia. Germinating spores may get fused together by their germ-tubes or branches arising therefrom.

In cultures, sclerotia are often developed. They are generally small and round but at times they have been observed to be as big as 1 mm. in diameter. In cross sections these sclerotia are found either to be a homogeneous mass of hexagonal or rectangular brown cells, or to be slightly differentiated into cortex and medulla, the central cells being large and thin-walled while the peripheral cells have a smaller lumen and thicker walls.

Glomerella stage.

Shear and Wood have found that if a culture from any particular acervulus or group of acervuli does not produce the ascogenous stage on corn meal at 75° to 85° F., it is useless to experiment further with material from the source¹; and they are of opinion that the perithecial forming faculty in the numerous cases of *Glomerella* studied by them is a fairly fixed hereditary character; because if once a race or strain which produces perithecia in culture media is obtained other generations from this strain or race continue to produce perithecia indefinitely².

Edgerton considers corn-meal-agar the most satisfactory medium for the growth of the fungi belonging to the genus *Glomerella*.

Krüger³ has found partly sterilized potato stems as particularly suitable for the development of perithecia. These and various other media have been tried for the development of the ascogenous stage not only of the chilli fungus but also of the *Carica papaya* anthracnose. It seems to me doubtful if the medium has any direct influence on the development of perithecia. What seems to be most essential is that a race or strain should be capable of producing the perfect stage. If once such a race or strain is obtained perithecia are formed on almost any medium, especially solid, at least for the first few generations. As will be seen later the perithecia forming faculty is not a fixed hereditary character which would ensure the development of perithecia indefinitely, as stated by Shear and Wood. Perithecial strains completely lose their spore-bearing faculty when their successive generations are cultivated for some length of time on the same medium and at room temperature. But, however, these sterile strains can be induced to form asexual spores by sudden change of food or temperature, e.g., subcultures on corn-meal, corn-meal-agar or sterilized chilli stem produce the conidial form when the transfers are made from a strain that has become sterile, through several generations having been cultivated on glucose-meat-extract-agar. Subcultures from sterile cultures on glucose-meat-extract-agar at room temperature, at times, develop the conidial form if they are kept in a hot incubator at 90° F. in winter, and in a cold incubator at 66° F. in summer. If three or four successive generations of these conidia-

¹ Shear, C. L. and Wood, A. K. Ascogenous Forms of *Glaeosporium* and *Colletotrichum*. *Bot. Gaz.*, XLIII, p. 262, 1907.

² Shear, C. L. and Wood, A. K. Studies of Fungous Parasites belonging to the Genus *Glomerella*. U.S. Dept. Agric., *Bur. Pl. Industry, Bull.*, No. 252, p. 72, 1913.

³ Krüger, F. Beiträge zur kenntnis einiger *Glaeosporium* I und II. *Abt. Kais. Biol. Anst. f. Land-u. Forstwirtschaft*, IX, 2, p. 217, 1917.

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producing cultures are cultivated on the same food and under the same conditions, they again become sterile. But, though the lost conidial form can be recovered, so far all attempts to get back the perithecial form from the strain which has lost it have been unsuccessful. What factor or factors influence the development of the perfect stage is not known.

Since 1914, *Glæosporium piperatum* E. and E. has been obtained in cultures on several occasions and cultivated on numerous kinds of media but the perithecial stage has been developed only on two occasions. In April 1915, perithecia were first formed on partly sterilized chilli stems. But unfortunately this strain was allowed to die out. In December of 1918, cultures of *G. piperatum* were taken from diseased chilli fruits in Burma by Babu P. C. Kar, Fieldman to the Imperial Mycologist, to whom my acknowledgements are due. Cultures on glucose-meat-extract-agar and on corn meal produced both the perithecial and *Glæosporium* forms at Pusa.

In the winter of 1916, the *Glomerella* stage was for the first time observed on diseased chilli fruits; a few fruits attacked by *Glæosporium piperatum* were incubated. The concentric rings of shining oily pink acervuli on one of the fruits were replaced in five or six days by an undulating, black, rugged crust in which were found the perithecia. In 1917 and 1918 perithecia were again found on a few incubated fruits attacked by *Glæosporium piperatum*.

The perithecial form found on these incubated fruits was identical with that previously produced in cultures of *Glæosporium piperatum* on partly sterilized chilli stems and on glucose-meat-extract-agar and that described by Miss Stoneman.

The perithecia found on the fruits (Fig. 4) are caespitose, membranaceous, pear-shaped with a short neck, dark brown in colour—light coloured towards the ostiole—situated on, or partly immersed in, a stroma of loosely inter-woven hyphae. They are not hairy, but the neck in some cases is slightly tufted. The perithecia resemble those of *Glomerella piperata* described by Miss Stoneman except that they are not hairy as figured by her.

Cultures taken from diseased fruits bearing perithecia have given the ascogenous stage. On maize-agar the perithecia are either scattered or aggregated together forming big black nodules like those of *G. frustigena* (Clint.) Sacc.¹ These on sectioning are found to be somewhat differentiated into cortex and medulla. The cortex is composed of large

¹ Edgerton, C. W. The Physiology and Development of some Anthracnoses. *Bot. Gaz.*, XLV, p. 387, 1908.

thin-walled cells lightly coloured, while dark-coloured small cells, compactly packed, form the medulla. Embedded in these nodules are perithecia in one or more layers.

In cultures the neck of the perithecium varies a great deal in length, it may be almost absent or as long as that figured by Miss Stoneman. Between these extremes there are all degrees of variation in the size of the neck. There is the same variation in the hairiness of the neck. It may be entirely smooth or it may have hairs sticking out from its sides in varying quantities. These characters are not constant even on the same medium and in the same cultures.

The asci are hyaline, sessile and as a rule clavate. The asci (Fig. 5 c) from the host generally measure between $45.0-66.0 \times 7.7-11.0\mu$; but on a fruit collected in November of 1918 the range of variation was between $49.5-93.5 \times 6.6-9.9\mu$. In the bigger asci the ascospores were arranged in a single row, one below the other (Fig. 5 b). In cultures there is the same range of variation in shape and size as that found by Shear and Wood¹ in the asci of *Glomerella rufomaculans* (Berk.) Spauld. and v. Sch. (= *Glomerella cingulata*). The ascospores (Fig. 7) are eight in number, hyaline, slightly curved, elliptical and generally sub-distichous, they measure $12.0-19.0 \times 4.4-6.6\mu$. They are quickly shed after maturity; the ascus wall rapidly disintegrates and the spores ooze out of the neck of the perithecium where they are held together in a drop of a shining viscous liquid. The ascospores germinate in water by giving out a germ-tube from near one of the ends; they may, at times, become septate; but they do not anastomose as do the conidia (Fig. 8). The germ-tubes after growing for some distance form an appressorium at the tip.

In old perithecia (from the host or from cultures) ascospores are found to lie scattered or in groups of eight as in the ascus but without the ascus wall which is invariably dissolved. They have, as a rule, become septate, generally once rarely twice, and their wall has distinctly turned pale brown. Ascospores that have germinated in the perithecium have been at times observed to have anastomosed by their germ-tubes. As already stated ascospores sown in water have not shown any of these changes even when kept for any length of time.

Miss Stoneman² who referred the perfect forms of *Glæosporium* and *Colletotrichum* to a new genus, *Gnomoniopsis*, is inclined to consider it as

¹ Shear, C. L. and Wood, A. K. Ascogenous Forms of *Glæosporium* and *Colletotrichum*. *Bot. Gaz.*, XLIII, No. 4, p. 263, 1907.

² Stoneman, B. A comparative Study of the Development of some Anthracnoses. *Bot. Gaz.*, XXVI, pp. 99-114, 1898.

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aparaphysate; von Schrenk and Spaulding¹ who later changed this name to *Glomerella* also describe it as aparaphysate; to Edgerton² it seems best to regard this genus as such; but Sheldon³ has seen paraphyses in a number of forms and Shear has found the asci of *G. rufomaculans* var. *vaccinii* Shear to be accompanied by what seem to be evanescent paraphyses. In the perithecia of chilli *Glomerella* are found at times sterile bodies (Fig. 5 a) of varying length and breadth but never longer or broader than the normal asci. They are not completely filled with protoplasm. It has, as a rule, contracted from the walls and become collected in the centre of these bodies. They can not be regarded as paraphyses because they seem to be asci which have become abortive at various stages of their development.

Miss Stoneman⁴ considers the perithecial form of *Glæosporium piperatum* E. and E. to closely resemble *Gnomoniopsis (Glomerella) cingulata* but makes a new species of the former as she finds a specific difference in its more slender perithecia and smaller spore measurements. At the same time she admits that these characters vary in different cultures and that the larger measurements of the perithecial stage of *G. piperatum* are common to smaller perithecia and spores of the privet anthracnose.

Miss Stoneman also lays importance to the difference in growth on nutrient media of the colonies from ascospores and conidia of the chilli and privet anthracnoses. From the later investigations of Edgerton⁵ and Shear and Wood⁶ it seems clear that much reliance should not be put on cultural characters for the determination of *Glomerella* species as they have found the perfect stage to be extremely variable.

That cultural characteristics and spore measurements are not a safe criterion in determining specific differences is also evident from the present study of the *Glomerella* on chilli. As already stated the perithecia and asci (Figs. 5 and 6) vary a great deal in size and shape; in many cultures the measurements of the asci and ascospores reached the limits given by Miss Stoneman for *G. cingulata*. It seems therefore that there

¹ Schrenk, H. von and Spaulding, P. The Bitter-Rot of the Apple. *U.S. Dept. of Agr., Bur. of Pl. Ind., Bull.*, No. 44, p. 29, 1903.

² Edgerton, C. W. The Physiology and Development of some Anthracnoses. *Bot. Gaz.*, XLV, p. 389, 1908.

³ Sheldon, J. L. The Ripe Rot or Mummy Disease of Guavas. *West Virginia Agr. Expt. Sta. Bull.*, No. 104, p. 312, 1906.

⁴ Stoneman, B. *loc. cit.*, p. 106.

⁵ Edgerton, C. W. *loc. cit.*, pp. 393-396.

⁶ Shear, C. L. and Wood, A. K. Studies of Fungous Parasites belonging to the Genus *Glomerella*. *U.S. Dept. of Agr., Bur. of Pl. Ind., Bull.*, No. 252, pp. 65 and 98, 1913.

are not sufficient reasons to consider the ascogenous stage of *Glæosporium piperatum* E. and E. to be different from *Glomerella cingulata* (Stoneman) Spauld. and v. Sch.

Development of Glæosporium and Colletotrichum acervuli in cultures of Glomerella.

In December 1918, a chilli fruit was found attacked by *Glæosporium piperatum* E. and E.; a week after it was incubated, the shining pink acervuli were replaced by a black, corrugated, rugged, carbonaceous crust. In this crust was found the ascogenous stage. A small bit from this perithecial crust was planted in a tube of glucose-meat-extract-agar. The growth remained sterile. In sub-cultures from this culture (which we shall call A) on sterilized chilli stems and on maize-meal-agar, conidia and perithecia were produced, but setae were invariably absent; but, however, sub-cultures on glucose-meat-extract-agar were sterile. Four months later, i.e. in April of the following year, sub-cultures from the sterile culture A were made on sterilized chilli stems (culture B) and on glucose-meat-extract-agar (culture C). In B the perithecial stage was produced, but not the conidial; while in C acervuli with or without setae were developed but no perithecia.

Thus all of a sudden the original sterile culture broke up into two different strains, one producing only perithecia on sterilized chilli stems and the other forming acervuli with and without setae on glucose-meat-extract-agar. These strains remained distinct only for a short time. The conidial strain soon lost its setae-producing faculty and developed the perithecia-forming faculty on glucose-meat-extract-agar. Subsequent sub-cultures on glucose-meat-extract-agar from these two strains were identical.

Sub-cultures from the perithecial strain, culture B, continued to produce perithecia, at first along with the *Glæosporium* stage, on various media, including glucose-meat-extract-agar. Eventually this strain produced only the perfect stage, without the conidial.

Sub-cultures from the conidial strain, culture C, on sterilized chilli stems, oat-juice-agar and maize-agar, at first, gave both the perithecial stage and the conidial, either with or without setae, but later only the perfect stage was produced on these media. Sub-cultures on glucose-meat-extract-agar, $\pm$ 5 Fuller's scale and neutral, and on bouillon agar, gave for some time only the conidial stage with and without setae. This tendency of developing only the conidial stage was lost by continuous sub-culturing on glucose-meat-extract-agar, and that of forming the

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perfect stage was developed. Sub-cultures from the original culture C, taken after a lapse of 2, 3, and 10 months on glucose-meat-extract-agar and other agar media, gave only the perithecial stage. Single spore cultures of ascospores and asci have produced only the perithecial stage, the conidial being absent.

From the behaviour of the chilli *Glomerella* in cultures it appears that *Colletotrichum nigrum* and *Glæosporium piperatum* are one and the same fungus, the conidial stage being generally without setae in Bihar (either the setae are developed only under certain conditions or only certain strains are capable of producing setae). The development of setae is not a constant feature of the genus *Colletotrichum*. The well-known bean disease *C. Lindemuthianum* forms pustules very often without the least trace of setae; in fact this bean anthracnose was first put in the genus *Glæosporium*. The same is true of the anthracnose on cucurbits. It was first named *G. lagenarium* but when setae were later found it was placed in the genus *Colletotrichum*. The anthracnose of tomatoes Chester¹ described in 1891 as caused by *C. lycopersici* n.sp. as there was an abundant development of setae in the acervuli, but in the following year the diseased spots were without setae and to all appearance the fungus was a *Glæosporium* and therefore Chester raises the question whether the presence or absence of setae is of sufficient generic importance to separate the two genera. Edgerton² considers the distinction between the *Glæosporium* and *Colletotrichum* so poor that he prefers to drop the name *Colletotrichum* in favour of *Glæosporium* in his discussion on the development of anthracnoses. According to Krüger³ *Colletotrichum* and *Glæosporium* cannot be sharply divided into two distinct genera and therefore he considers *Colletotrichum* as a sub-genus. Miss Stoneman⁴ has found the presence of setae so variable as to doubt whether they form a well-founded basis for distinguishing these two genera. Shear and Wood⁵ are also of the same opinion. They have found setae in the acervuli in one part of a pure culture, whereas in other parts of the same culture they were absent. They⁶ have also found this same variation occurring upon leaves, especially in the form found upon cranberry.

¹ Chester, F. D. *Delaware Station Report for 1891*, pp. 60-63 and for 1892, p. 80.

² Edgerton, C. W. *Loc. cit.*, p. 369.

³ Krüger, F. *Loc. cit.*, p. 303.

⁴ Stoneman, B. *Loc. cit.*, p. 70.

⁵ Shear, C. L. and Wood, A. K. *Ascogenous Forms of Glæosporium and Colletotrichum*. *Bot. Gaz.*, XLIII, p. 263, 1907.

⁶ Shear, C. L. and Wood, A. K. *Studies of Fungous Parasites belonging to the Genus Glomerella*. *U.S. Dept. Agr., Bur. Pl. Ind., Bull.*, No. 252, p. 64, 1913.

Even in single-spore cultures some acervuli show many setae, others a few and still others none.

Colletotrichum nigrum E. and Hals.

The acervuli of *C. nigrum* E. and Hals. on chilli fruits collected in Burma and in Pusa are quite similar to those of *G. piperatum* E. and E. already described, except that in the acervuli of the former there is a development of stiff, erect dark brown setae, which measure up to 150μ long and 4μ broad.

In December 1918, a chilli fruit was found in Pusa attacked by *C. nigrum*. The acervuli were carefully examined under a binocular microscope and all of them, without exception, were found to have developed setae. Four series of cultures from this diseased fruit were started on glucose-meat-extract-agar.

1. A single conidium was planted on the medium.

2. A diseased seed was aseptically removed and transferred to the medium.

3. It may perhaps be suspected that the fruit might have been infected with *G. piperatum* E. and E. as well, the acervuli of which had escaped detection under the microscope, that the single conidium might have been taken from a *Glæosporium* acervulus and that in the tissues of the diseased seed both *Glæosporium* and *Colletotrichum* hyphae might be present. To be sure that only *C. nigrum* was really taken in culture a single seta was picked off and planted on the medium.

4. The infected fruit was incubated and in less than a week a thick, black, undulating crust was formed where there were originally acervuli of *C. nigrum*. In this crust were found perithecia. A single ascus was transplanted on the medium. (This development of the perfect stage is similar to that already described in the case of *G. piperatum*.)

A fifth series was at the same time started, for comparison, from a single ascus got from a fruit originally attacked by *G. piperatum* E. and E. and which had developed the ascogenous stage on incubation.

At room temperature, which ranged between 62° to 68° F., the growth in all these five series of cultures was alike. The mycelium was matted and confined to the substance of the medium and at first the colour of the mycelium on the surface of the slant was distinctly pink, but there was no development of conidia except in the culture started from a single seta, Ser. 3rd; there were no setae in this culture. The pink colour was soon replaced by black or greenish black. In a week's time the surface of the medium was covered by a thick undulating black crust, punctuated

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by small raised dots or pinheads; this crust was the stroma in which were wholly or partly immersed perithecia. In later subcultures, the pink colour of the young mycelium was completely absent.

A second lot of cultures from the above five series was at the same time incubated at a temperature of 89·6° F. The growth in all these cultures was again identical but different from that described above. On the upper drier part of the medium it was fluffy, but on the rest of the slant the growth was slightly aerial and the aerial mycelium had formed white feathery strands. The colour of the slant was distinctly pink, relieved occasionally by appressed black strands or black dots, which were immature perithecia. On the sides of the medium there was a development of black stroma which contained acervuli without setae, conidia were also produced on the tips of hyphae but in no part of the cultures were setae developed. The acervuli and conidia were similar to those of *G. piperatum* E. and E.

In cultures on corn meal at first the conidial stage was developed which was later replaced by the perithecial; all these cultures were identical in appearance but the one originally started from a single seta formed setae in some of the acervuli which were produced in large numbers while in the other cultures acervuli were few and without setae.

The perithecia and asci on the host and in cultures are exactly similar to those already described. They show the same range of variation as regards the size and hairiness of the perithecial neck and the size of the asci as that shown by the perithecia and asci of *Glomerella cingulata* (Stoneman) Spauld. and v. Sch., the perfect stage of *Glæosporium piperatum*. The asci (Fig. 14) from the host measure 44·0–82·5 $\times$ 9·9–12·1 μ , and the ascospores measure 15·4–19·8 $\times$ 5·5–6·6 μ . The asci are slightly bigger than those generally found on the chilli fruits infected by *G. piperatum* but they are of the same size as those found on a fruit last year (cf. Fig. 4). The bigger size of the asci is due to the disposition of the ascospores in a single row one below the other.

The ascospores in size and shape are similar to those already described: in old perithecia the ascospores have been found to have become septate and to have coloured brown.

The fungus grows luxuriantly in winter at room temperature—62° to 69° F.—and develops perithecia but the ascospores do not germinate either in water or in nutrient media at this temperature; however they readily do so when incubated at 89·6° F.

With the development of the perithecial stage, *Glomerella cingulata*,

from *Colletotrichum nigrum* E. and Hals. the life-cycle of *G. cingulata* has been completed. We have seen that

(1) *Glomerella cingulata* has been produced in cultures of *Glæosporium piperatum* E. and E. on partly sterilized chilli stems.

(2) Acervuli with and without setae, *i.e.* *Colletotrichum* and *Glæosporium* forms, and the perithecial stage have been formed in cultures started originally from a perithecium from a chilli fruit which developed the perfect stage after it had first been attacked by *Glæosporium piperatum*.

(3) Acervuli without setae and the perithecial stage, identical with *Glomerella cingulata*, have been formed in cultures started from (a) a single conidium of *Colletotrichum nigrum* E. and Hals. and (b) a single ascospore from the perithecial stage developed after incubating the chilli fruit attacked by *C. nigrum*; and acervuli with and without setae and perithecia have been produced in cultures started from a single seta of *C. nigrum*. Therefore, now there seems to be no doubt that *G. piperatum* and *C. nigrum* are forms of the same fungus and that the ascogenous stage is *Glomerella cingulata* (Stoneman) Spauld. and v. Sch.

That *Colletotrichum* and *Glæosporium* on chillies are one and the same fungus is also seen from the study of the conidial forms of the *Glomerella* on *Carica papaya*, which is identical with the chilli *Glomerella*. Single spore cultures started from *Glæosporium* and *Colletotrichum* acervuli have given identical growth; in both these cultures the perithecial stage and the conidial without setae were developed. In subsequent subcultures the conidial stage was lost. Cultures started from single asci and single ascospores have produced only the perithecial stage, as in the case of the chilli *Glomerella*.

Variability of the fungus.

The strains obtained from fruits attacked by *Glæosporium piperatum* E. and E. have been cultivated on various media and under varying conditions for months on end but very great or sudden variations have never been observed. As already stated, by continuous subculturing on glucose-meat-extract-agar the conidia bearing faculty was gradually lost and the cultures became sterile. But if these sterile cultures were transferred to sterilized chilli stems, the conidia forming capacity was regained and in subsequent transfers on glucose-meat-extract-agar conidia were formed for two or three successive generations after which the fungus again became sterile. It was however found that this process of getting the conidial stage could not be carried on indefinitely. The

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loss of the conidia bearing faculty was ultimately complete and transfers on sterilized chilli stems gave only sterile aerial growth. But in the cultures made from the perithecial strain of *Glæosporium piperatum* incredibly large and very often sudden variations have been obtained as will be seen from the account given below. Such large variations have been observed by Edgerton¹ as well in cultures of *Glomerella* causing the bitter rot of apples. These variations consist of the absence or presence of perithecia, absence or presence of acervuli, absence or presence of setae and development of aerial hyphae or of hyphae matter and confined to the substance of the medium.

In subcultures on sterilized chilli stems and maize-meal-agar from the original sterile culture, which we have called A on page 253, acervuli without setae and perithecia were freely formed, and subcultures on glucose-meat-extract-agar from these perithecia bearing cultures also gave the perfect form in addition to the *Glæosporium* form. But in subcultures on glucose-meat-extract-agar direct from the sterile culture A the growth was sterile and confined to the surface. On the 30th of April and 2nd of May, 1917, two subcultures, GIC₁ and GIC₂, were made on glucose-meat-extract-agar from the original sterile culture A of December 1916. The first sudden variation or mutation was obtained in these subcultures. The growth in both was similar to each other but was radically different from that of the parent culture. In these cultures a black stroma was produced in which were formed acervuli with and without setae. No perithecia were produced. From GIC₁ a subculture, GIC₃, was made on the same medium on 7th May, 1917, and it was similar to its immediate parent. These three series were kept going for a long time. They showed remarkable variations from time to time. For the first two or three months they continued to produce the conidial form, but they lost this as suddenly as they gained it, and it was replaced by the perithecial stage.

GIC₁ continued to produce perithecia on glucose-meat-extract-agar till March 1918. In a subculture made on the same medium on the 16th of that month a culture two months old only acervuli with and without setae were formed and not perithecia. In the subsequent three or four subcultures the conidia continued to be formed but this stage was suddenly lost in the subculture made in the end of April. The fungus in this subculture was sterile but the growth was not similar to the original sterile culture A, but was similar to the sterile culture of *Glæosporium piperatum*. The aerial growth was moderate and covered a black or

¹ Edgerton, C. W. Physiology and Development of some Anthracnoses. *Bol. Gaz.*, XLV, p. 395, 1908.

greenish black stromatic substratum formed on the surface of the medium. Subsequent subcultures on glucose-meat-extract-agar remained sterile—these cultures were kept running for over a year; but in April, 1918, subcultures on sterilized chilli stems and on corn-meal-agar perithecia were developed but not acervuli. A subculture on glucose-meat-extract-agar from the perithecia-bearing culture on sterilized chilli stems gave only the conidial stage without setae; but transfers on glucose-meat-extract-agar from the perithecial culture on corn-meal-agar were sterile. From this sterile culture transfers were made in May, 1918, on a liquid medium containing $(\text{NH}_4)\text{NO}_3$ (1 per cent.), $\text{KH}_2(\text{PO}_4)$ (.5 per cent.), NaCl (.6 per cent.), MgSO_4 (.25 per cent.), traces of FeCl_2 , CaCl_2 and MnSO_4 and Glucose (3 per cent.) in 100 c.c. of water. On the surface of the liquid a thick crust pink and black in colour was formed; no fructification was produced. A subculture from this on glucose-meat-extract-agar produced pink acervuli. Setae were exceedingly rare. A culture grown on glucose-meat-extract-agar started from the sterile culture on the same medium, two months old, on the 8th May produced acervuli with setae embedded in a dark black stroma.

On brinjals inoculated in June, 1918, with the sterile culture perithecia were produced. Subcultures on corn-meal in April, 1919, from the sterile culture on glucose-meat-extract-agar which was kept running for a year, acervuli with and without setae were found but no perithecia. In subcultures on glucose-meat-extract-agar from the culture on corn-meal in April, 1919, acervuli with and without setae were produced. On corn-meal-agar subculture made in June, 1919, gave acervuli with and without setae.

From one of the perithecia-bearing cultures of GIC₂ subculture was made on bouillon agar on the 21st February, 1918: the resulting growth was sterile. From this sterile growth a transfer was made on glucose-meat-extract-agar. The growth of the fungus in this subculture was identical with that of the sterile fungus in the original culture A. In subsequent transfers on glucose-meat-extract-agar the fungus was sterile and formed matted hyphae on the surface of the medium; greenish black strands of hyphae, especially near about the inoculum, were developed. On chilli seedlings aseptically grown in tubes on moist cotton plugs inoculated with this sterile fungus perithecia were produced. On corn-meal-agar inoculated on the 24th April, 1918, perithecia and acervuli without setae were developed, while on sterilized chilli stems inoculated at the same time and from the same culture only sterile aerial growth was obtained. Subculture on glucose-meat-extract-agar made on the 7th

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May from the fertile growth on corn-meal-agar was sterile. In a liquid medium containing $(\text{NH}_4)_2\text{NO}_3$ (1 per cent.), $\text{KH}_2(\text{PO})_4$ (·5 per cent.), MgSO_4 (·25 per cent.), traces of FeCl_2 and MnSO_4 and maltose (3 per cent.) in 100 c.c. of water, inoculated with the sterile strain, the growth was sterile but the subculture from this, made on the 2nd May on glucose-meat-extract-agar, gave acervuli without setae. From this fertile strain the next generation on the same medium also developed acervuli without setae, but in the subsequent subcultures no fructification was developed.

In April, 1919, subcultures on corn-meal from the original sterile culture on glucose-meat-extract-agar which was kept going for a year were sterile but were not in appearance different from the cultures GIC_1 and GIC_3 of the same date on the same medium. Subcultures in May, 1919, on glucose-meat-extract-agar, were sterile: there was stroma formation from which setae were developed but no conidia. On corn-meal-agar acervuli with and without setae were produced.

GIC_3 , which was a direct progeny of GIC_1 , continued to develop perithecia longer than its ancestor and it did not lose the perithecial forming capacity on glucose-meat-extract-agar as suddenly as GIC_1 and GIC_2 . In subcultures made in February and March, 1918, perithecia were not produced all over the agar medium as in the previous cultures but they were confined to the neighbourhood of the inoculum and their presence was marked by a dendritic growth of the perithecial stroma. As the inoculum was generally placed on the upper and therefore drier part of the slant, it was supposed that the amount of moisture determined the perithecial formation. To verify this supposition some slants were inoculated on the lower moist part and some on the drier upper part. One set of these inoculations were placed in a moist chamber in order to keep the moisture even and a duplicate set which served as a check was kept under ordinary conditions. The growth of the perithecia in both these sets continued to be poor and to be confined to near about the inoculum. In the subculture on glucose-meat-extract-agar made in the beginning of April, 1918, the perithecia were absent and the growth was sterile. But in the subculture made from this sterile race on the 24th of the same month there was a copious formation of acervuli with and without setae, but there were no perithecia. The next generation from this acervuli-producing fungus was sterile though it had all the appearance of the culture-bearing perithecia: subsequent subcultures on glucose-meat-extract-agar continued to produce conidia for only a year; setae were absent. The perithecia-forming faculty on this medium

was completely lost. From the sterile culture of April subcultures were grown on corn-meal-agar on the 24th April, 1918. Perithecia were abundantly formed: in the subculture from this perithecial race on glucose-meat-extract-agar the growth was again sterile. Inoculations on sterilized chilli stems and living chilli seedlings aseptically grown in tubes on moist cotton plugs gave a copious crop of perithecia, while on brinjals and peaches only acervuli without setae were developed. Subcultures on glucose-meat-extract-agar in May, 1918, from the perithecial strain on sterilized chilli stems gave only the conidial form without setae.

Subcultures on corn-meal, in April, 1919, from the fungus cultivated for over a year on glucose-meat-extract-agar developed only acervuli with and without setae, and in transfers on glucose-meat-extract-agar acervuli with and without setae were produced but not the perfect form. Subcultures in June, 1919, on corn-meal-agar gave only conidia without setae.

INOCULATION EXPERIMENTS.

It seems doubtful if inoculation experiments are of much value in establishing the relationship of the chilli *Glomerella* with the other species of this genus or in finding the range of hosts of the chilli fungus, as the success or failure of inoculations depends on so many factors, all of which may not be controllable. Different strains or races vary not a little in virulence, *e.g.*, three strains isolated from a culture, originally started by planting perithecia on a nutrient medium, *viz.*, (1) conidial, (2) sterile, (3) perithecial, showed distinct variations in their effects on chilli seedlings grown aseptically on moist cotton plugs in tubes. The perithecial race killed the seedlings in a fortnight and the sterile acted more slowly: and in both cases perithecia were developed on the inoculated seedlings; the conidial strain, however, infected the seedlings very slightly and no fructification was produced, even in three weeks. But the strain taken in culture from diseased fruits giving only the *Glucosporium* stage, which develops in nutrient media only this conidial form, has more virulent infecting power than the strain got from perithecia. Not only is there variation in the virulence of the different strains but there is also variation in the susceptibility of the host, *e.g.* inoculations on banana fruits have given varying results, some fruits being more readily infected than others. Conditions of temperature and moisture also play an important part in the successful inoculation of the host. Again, in the experiments in which fruits were used for the inoculation experiments it was at times

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difficult to decide if the fungus was growing on the inoculated host as a parasite or on account of its loss of vitality the fruit merely served as a nutrient medium for the saprophytic growth of the fungus, *e.g.* the *Glæosporium* strain was inoculated on apples through a puncture. In four days a slight brown depression round the inoculum was visible but the infection showed signs of increasing only after 25 days and a few days later the major part of the fruit was sunken and brown, the diseased area showed acervuli of the *Glæosporium* type. These results of the inoculation can be interpreted in two ways, (1) the infection had really occurred as was shown by the brown depression, but the fungus did not develop further at the time for lack of proper temperature or moisture, (2) the slight brown depression was due to the death of the cells as a result of the puncture and the hyphae had entered the cells after they were dead, and only when the vitality of the fruit was impaired by long storage was the fungus able to grow further.

This great variability in virulence is found not only in the *Glomerella* of the chilli but it seems to be a characteristic of this genus, judging from the researches of Barrus¹, and Shear and Wood².

The results of the inoculations are given below. In all these experiments conidia or mycelium from the cultures giving only the *Glæosporium* stage and originally started from a single spore taken from a *Glæosporium* acervulus from a diseased chilli fruit were used, unless where otherwise stated.

Chillies.

Inoculations on fruits have been made on various occasions and the results have not been uniform. Wound inoculations take more readily than surface inoculations and fruits almost ripe or wholly ripe are more susceptible than unripe fruits. The local varieties are more susceptible than the Peshawar variety. As a rule, in a couple of days after the inoculation of the fruit with the *Glæosporium* form, a black depression is produced round the inoculum which increases in size concentrically. At first pink acervuli are formed in the black depression but later they appear even beyond the discoloured area. Sometimes there is no external sign of the inoculation having succeeded till small raised points appear on the red surface of the fruit. These raised points are the immature acervuli. In some cases the infection remained very localised.

¹ Barrus, M. F. Variation of Varieties of Beans in their Susceptibility to Anthracnose. *Phytopathology*, 1, No. 6, p. 195, 1911.

² Shear, C. L. and Wood, A. K. Studies of Fungous Parasites belonging to the Genus *Glomerella*. U.S. Dept. of Agr., Bul. Pl. Ind., Bull., No. 252, p. 74, 1913.

When the perithecial form or the sterile and the conidial strains (forming acervuli with and without setae) developed from the perithecial form were used for inoculating fruits the infection took very slowly. At times immature perithecia or sclerotia were developed a week or ten days after the fruits were inoculated; acervuli with and without setae were formed only in isolated cases. At times the infection remained confined to a very limited area round the inoculum. In some cases where the infection had spread almost over the whole fruit (as was evident from the discoloration of the skin and the seeds and the presence of hyphae in the loculi of the fruits) still no sort of fructification was developed. In some cases the inoculations had completely failed. Even in the same set of experiments there were varying degrees of the extent of the infection.

Microtome section of inoculated chilli fruits show that the hyphae or germ-tube can penetrate unbroken cuticle. An appressorium is formed at the tips of an hypha or germ-tube. This appressorium lies closely appressed to the cuticle and puts forth a very fine process or germ-tube which is capable of piercing the cuticle. The process within the cuticle either remain fine or becomes swollen (Fig. 1).

Inoculations on growing points of mature plants and flower-buds and flowers were tried only with the strain giving the *Glæosporium* stage; growing points were only slightly infected and that too only under extremely moist conditions. Flower-buds and flowers were readily infected but the infection did not spread beyond the flower-stalk: acervuli were formed in a few days after inoculation.

Inoculations on seedlings grown aseptically on sterilized cotton plugs have already been described above.

Carica papaya.

Flowers and very small fruits, those that have not turned green, take the infection very readily. The first sign of successful infection on the flower is evident by the browning of the tissues in the neighbourhood of the inoculum. This browning extends very rapidly and the whole flower is soon covered with *Glæosporium* acervuli. On the fruits which are whitish yellow in colour or are just beginning to turn yellow successful inoculations have been secured through the scars of the fallen floral leaves or through the decaying styles. At the point of inoculation a circular depression is noticeable in twenty-four hours. This depression extends concentrically and in three or four days the whole fruit is infected. Fruits that have just turned green take the infection only through wounds, and that too not very readily. From the infected tissues

latex exudes in tiny drops. Larger fruits could not be inoculated. When the strain that produces only the *Glæosporium* stage was used for inoculations, *Glæosporium* acervuli were developed on the infected tissues, but if the perithecial strain was used, generally either immature perithecia or sclerotia were formed, rarely acervuli.

Pods of *Dolichos lablab* and *Vigna catjang* take the infection through wounds. At times, the infection at first remains localised for some days and then spreads further.

Mature fruits of tomatoes and brinjals have been inoculated through wounds. As the result of the inoculation soft rot was produced. Brinjals were inoculated with the *Glæosporium* form and the perithecial. In both cases *Glæosporium* acervuli were produced.

Inoculations with apples have been partially successful as stated above. Ripe fruits of peach have been successfully inoculated with the perithecial form. *Glæosporium* acervuli were formed.

Small plants of sweet peas inoculated by bruising the epidermis wilted and developed *Glæosporium* acervuli in about ten days.

Inoculations through punctures on fruits of *Citrus* sp. produced a sort of a wet rot in about a week. *Glæosporium* acervuli were developed in the brown rotting tissues.

Inoculations on onions (*Allium* sp.), sugarcane and jowar leaves, mango fruits, pods of *Phaseolus vulgaris*, have been unsuccessful.

Anthracnose of Carica papaya.

On this host the disease is to be found on flowers, fruits and flower-stalks. It has not been observed on leaves and on living stems at Pusa, though *Colletotrichum* sp.¹ has been recorded on leaves and stems, and also on fruits in Barbados.

Diseased flower-buds do not open but turn brown, become dry and soon fall off. The diseased parts are punctuated by small dots which are at first pink in colour but later they turn black or brown. If the infection takes place when the floral whorls have opened, the diseased floral leaves turn brown and wither. From these leaves the disease may travel to the base of the ovary and to the flower-stalk.

The most critical period when the fruits get infected is when they are newly set, when the pale whitish yellow colour is still persistent and when they are not in latex. A considerable amount of damage is also done to the fruit after it has turned distinctly green and after the laticiferous tissues are developed. Such fruits are generally infected

¹ *Agricultural News*, xiv, No. 341, p. 174, 1915.

when they are not more than about two inches in length. Bigger unripe fruits are very seldom infected. Fruits that have begun to turn yellow and ripe at times get diseased. But the percentage of the loss of big fruits is negligible.

The infection of the newly set and young green fruits takes place generally either through the stigmas or through the scars left by the floral leaves. If the infection starts from the stigmas the fruit shows a pinched-in appearance. If it starts from the scars left by the fallen floral leaves the base of the fruit becomes sunken and the depression runs into folds and the fruit generally becomes flattened out. The infection can also take place through punctures on the skin. Where there is the infection there appears a circular saucer-shaped depression in the skin. This depression increases concentrically with the progress of the disease. The fruit ultimately completely loses its normal shape. The diseased young fruit loses its green colour and becomes pale yellow, green or white yellow. From the centre of the diseased spots latex exudes in tiny drops. On the newly set fruit, which is still whitish yellow in colour, the infection may also start through its uninjured walls where the presence of the disease is marked by a circular depression which increases in diameter along with the growth of the fungus. If fruits which are about to ripen become diseased, it has been found as a rule that the infection starts from several points which are visible in the early stage as round water-soaked depressions. These diseased areas do not merge into each other but get delimited by a ridge being formed between the neighbouring depressions. In rare cases a single infection spreads over the whole fruit. The diseased area grows concentrically; the old infected tissues are thrown off in dry flakes.

The diseased fruit, especially the very young fruit, becomes mummified, hard and woody, and soon loses its normal shape. If the fruit is cut through a diseased spot the infected tissues are sharply demarcated from the healthy tissue. The diseased part in section is crescent-shaped, dry and pale white in colour which is very conspicuous if the fruit be ripe. The white diseased sunken tissues can be lifted off with a pointed instrument.

The diseased areas when fresh are generally found to be fleshy pink in colour and moist, due to the presence of innumerable acervuli. The acervuli on drying either remain pink coloured or turn black from margin inwards. Till lately, the acervuli were found without setae. But diseased fruits examined in 1917 have shown the presence of setae. Diseased spots with and without setae are as a rule distinct from each other and

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the former are distinguished from the latter by their black and bristly appearance; but in some cases acervuli with setae have been observed to have developed on incubation in diseased spots which had formerly acervuli without setae. The same has been observed in the case of the acervuli of the *Glomerella* on chillies. On only two or three occasions has the perfect form been found on the fruit. This form has been observed to develop in the old diseased spots in which were formerly the acervuli. The pink colour of the acervuli without setae is lost by degrees and changes into black as dark brown coloured hyphae begin to develop from margin inwards. Ultimately the concentric arrangement of the acervuli in the diseased spot is lost and the once round and sunken spot becomes covered by an undulating rugged and carbonaceous crust. The gradual change due to the development of the perithecia is not so well marked in the spots having acervuli with setae on account of the black colour. The formation of the perithecial stage becomes noticeable by the presence of the undulating rugged crust.

Fruit stalks.

The disease extends to the fruit stalk from the infected fruit but in a few cases the infection has been observed to originate from the stalk. The diseased stalk becomes dry and hard as does the diseased fruit. These dry stalks with the dead fruits remain hanging on the tree for a long time after they are mummified. So far, the acervuli on the stalks have been found without setae. They are not crowded together or confined to a definite area as on the fruit but they are scattered.

Sections through a diseased spot show that in the development of an acervulus there is at first in the epidermal and subepidermal cells a collection of hyphae which form a distinct stroma of pseudo-parenchymatous cells before conidiophores are developed as in the case of chilli *Glucosporium*. This stroma is at first hyaline but later turns brown from the margin inwards. The stromatic cells are uninucleate. Conidiophores are developed from the uppermost cells of the stroma. They are hyaline and broad at the base but tapering at the end (Fig. 9). From the tips of the conidiophores uninucleate elliptical and hyaline spores are cut off in succession. If sections are made through a diseased portion bearing the perfect stage, perithecia are found seated on or partly immersed in a stroma of loosely interwoven brown hyphae. The neck is usually very distinct but this part of the perithecium is very variable in size. At times it is markedly hairy, as hairy as the perithecia of the chilli *Glomerella* figured by Miss Stoneman; in some cases the neck is

slightly tufted, while in others it is untufted. The perithecia are flask-shaped, caespitose, membranous and dark brown in colour. They measure $315.7-385 \times 123.2-292.6\mu$.

The asci (Figs. 10, 11 and 12) are sessile and clavate and measure $60.0-93.5 \times 88-12.1\mu$.

The ascospores (Fig. 13) are hyaline, slightly curved, subdistichous and elliptical. They measure $13.2-20.9 \times 4.4-6.6\mu$. In old perithecia the ascus wall has been found to be disintegrated, setting free the ascospores. In these old perithecia the ascospores are found to be empty of their protoplasmic contents and to have become septate, generally once and rarely twice, and their walls have turned distinctly pale brown in colour, as in the case of the chilli *Glomerella*.

The perfect stage of the *Carica* anthracnose is identical with the chilli *Glomerella* in both morphological and cultural characteristics.

SUMMARY.

Glaosporium piperatum E. and E. and *Colletotrichum nigrum* E. and Hals. are not known to be destructive to chillies in India but they cause much loss of fruit in Burma.

These fungi are considered to be identical and to be the conidial forms of *Glomerella cingulata* (Stoneman) Spauld. and v. Sch., which is shown to be synonymous with *Gnomoniopsis (Glomerella) piperata* Stoneman, the ascogenous stage of *G. piperatum* E. and E., according to Miss Stoneman.

The perithecia-producing faculty does not depend on the nutrient medium on which the fungus is grown but depends on the race or strain.

This faculty is not a fixed hereditary character but is lost by cultivating successive generations on the same medium at room temperature.

There is a great deal of variation in the size and hairiness of the neck of the perithecium and in the size and shape of asci, and therefore cultural characteristics cannot be much relied upon for determining the species.

The perithecia are aparaphysate.

The ascospores are hyaline, unicellular and slightly curved, but in old perithecia they are found to be septate and their walls coloured brown.

In cultures the presence of setae is not a constant character.

In cultures of the perithecial strain there are very often sudden variations in the characters of the growth of the fungus.

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It is doubtful if inoculation experiments are of much value in establishing the relationship of the *Glomerella* on chillies with the other species of this genus or in finding its range of hosts, as the success of inoculation depends on several factors all of which may not be controllable.

Inoculations on chillies, *Carica papaya*, and other plants have been described.

A new disease of *Carica papaya* is described. It is caused by the conidial forms of a *Glomerella*, which is identical with that on chillies in both morphological and cultural characteristics.

The disease is found on flowers, young fruits and fruit stalks. Diseased flower-buds do not open but fall off. If the infection takes place when the flower whorls have opened they turn brown and wither.

The most critical period when the fruits get infected is when they are newly set. Older fruits also at times get diseased.

Newly set and young fruits get the infection through their stigmas or through the scars of the floral leaves or through punctures on the skin.

The infection is marked by the presence of a circular saucer-shaped depression in the skin.

Diseased fruits become mummified, hard and woody.

The study of the conidial forms of the *Glomerella* on *Carica papaya* also shows that *Glaeosporium* and *Colletotrichum* are one and the same fungus.

EXPLANATION OF PLATE X

Figs. 1 to 8. *Glaeosporium piperatum* on chillies and its perfect stage *Glomerella cingulata*.
Fig. 1. Transverse section of a chilli fruit showing the penetration of the germ-tubes from appressoria. $\times 421$.

Fig. 2. Acervulus of *Glaeosporium* on a chilli fruit. $\times 256$.

Fig. 3. Germination of conidia. $\times 418$.

Fig. 4. Perithecia of *Glomerella piperata*. $\times 88$.

Figs. 5 and 6. Asci showing variation in size. $\times 418$. Fig. 5 (a) a group of asci from a culture, b and c asci from the host. Fig. 6, asci from inoculated chilli seedlings.

Figs. 7 and 8. Ascospores, $\times 418$, and their germination $\times 53$.

Figs. 9 to 13. *Glomerella cingulata* on *Carica papaya*.

Fig. 9. Acervulus on a *Carica* fruit showing uninucleate cells. $\times 553$.

Figs. 10 and 11. Asci from culture. $\times 418$.

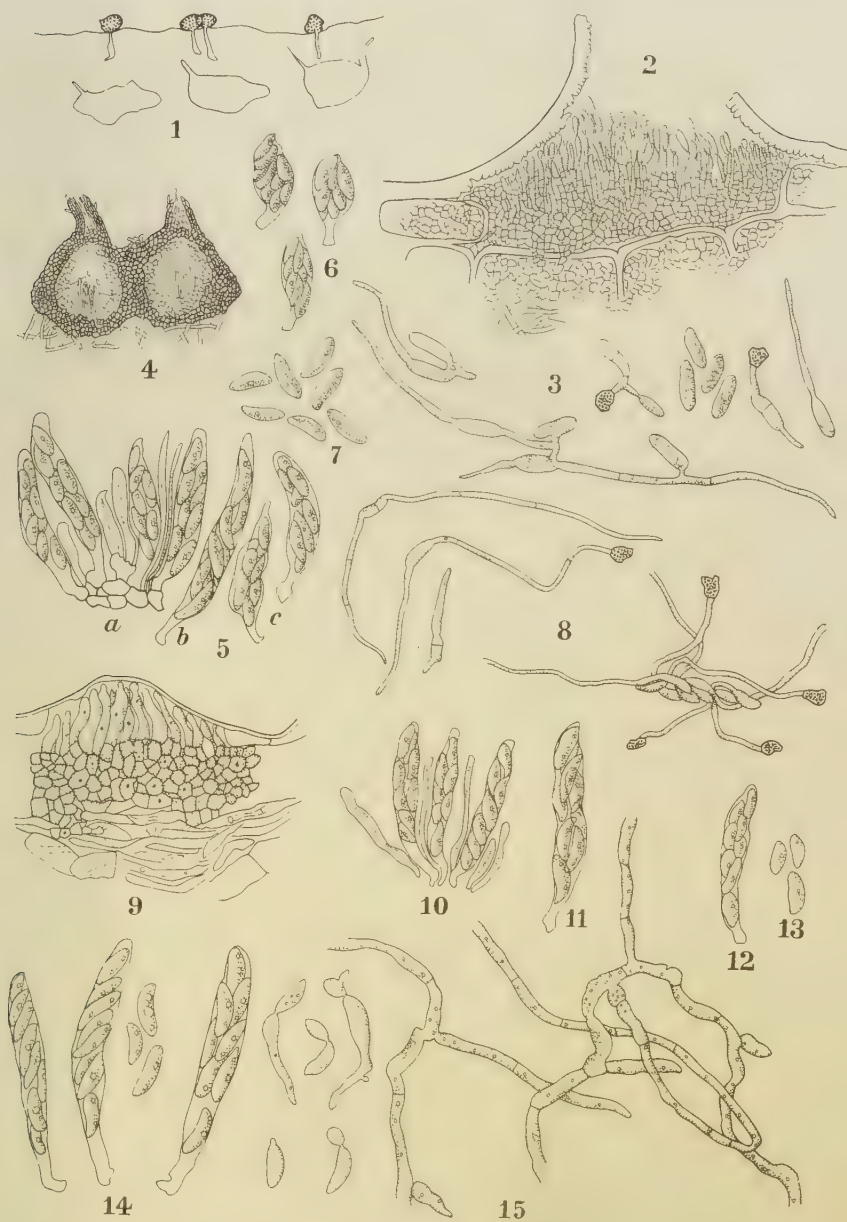
Fig. 12. Asci from a *Carica* fruit. $\times 418$.

Fig. 13. Ascospores. $\times 418$.

Figs. 14 and 15. *Glomerella cingulata* the perfect stage of *Colletotrichum nigrum* on chillies.

Fig. 14. Asci and ascospores. $\times 418$.

Fig. 15. Germination of ascospores. $\times 418$.



FIELD EXPERIMENTS ON THE CHEMOTROPIC RESPONSES OF INSECTS.

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(With 1 Text-figure.)

PART I.

PRELIMINARY EXPERIMENTS.

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I. INTRODUCTORY REMARKS.

A SURVEY of the literature of applied entomology brings home the fact that the efforts of economic entomologists have been largely confined to the discovery of the means of destroying injurious insects; to studying their life-histories, and to ascertaining the most vulnerable stage thereof for the application of remedial measures. During the last few years artificial means for the destruction of noxious insects have progressed rapidly, and even the comparatively recent methods of combating them by the agencies of parasites have made remarkable advances. In all that has been achieved, however, it is evident that the scientific aspects of investigation have constantly been sacrificed in the interests of results derived by empirical methods. Insecticides are used throughout the

world and yet we scarcely possess any knowledge as to how they act. Since 1787, when the Abbe Roberjot first discovered the method of destroying the vine moth (*Sparganothis pilleriana*) by means of light, the application of this method has developed rapidly, and there are now in existence ingenious traps, elaborate lanterns and even expensive and complicated electric installations; but strange as it may seem, it was not until 1904 that the study of the effects of light of different colours, in attracting insects, was first taken up by Perraud. Even to this day our knowledge of the physical side of the subject is far from adequate; much research is also needed with regard to the influence of meteorological conditions, and we know comparatively little concerning the proportion of the sexes of the insects attracted. Chemotropism has shared no better fate, and we are largely in the dark as to the influence of the various constituents of those baits extensively used by economic entomologists. Molasses forms one of the most important ingredients, but we are totally ignorant as to which constituent (or constituents) of this complex substance exercises chemotropic properties. Dewitz (1912), Tragardh (1913) and Imms (1914) have emphasised the need for physiological research in applied entomology, but such research they insist must be carried on with a broader outlook than that of modern applied entomologists. The possibilities that the investigation of chemotropism offers, both as regards the application of results achieved and the advancement of scientific knowledge, can be well appreciated by reference to the work of Verschaffelt (1910), Howlett (1912, 1914, 1915), Barrows (1907), Richardson (1916, 1917) and others. There is hardly any doubt that one of the most promising aspects of applied entomology lies along these lines and, as will be pointed out on a later page, in chemotropism we should seek for new and effective measures for combating insect enemies. The control of the house-fly supports this contention, but we are only at the threshold of an extensive line of investigation.

The present paper only embodies observations of an essentially preliminary nature and were carried out by M. A. Husain at the suggestion of the senior author (A. D. Imms); the interpretation of the results and the writing of this article is a conjoint production. Delay has been inevitable in the preparation of this paper owing to one author being transferred to India, while the other was located at the Rothamsted Experimental Station, Harpenden. The necessary laboratory work was conducted in the Department of Agricultural Entomology, Manchester University. We are greatly indebted to Messrs C. G. Lamb, P. H. Grimshaw and H. Bury for help in identifying numerous specimens of Diptera.

II. GENERAL AND HISTORICAL.

Chemotropism is the response of an organism to the stimulus of chemical substances manifested, if the stimulus be responded to, in movements towards (positive chemotropism) or away (negative chemotropism) from the source of stimulus. Dewitz (1912) was the first to emphasise the importance of the study of tropisms in relation to applied entomology and dealt largely with phototropism. Tragardh (1913) laid stress upon chemotropism and pointed out possibilities of its application in combating destructive insects. There is no doubt that various tropisms play a vital part in the economy of insect life but, of these, chemotropism is the great controlling factor. The phenomenon is particularly evident in the search for food, in the pursuit of the sexes and the selection of suitable breeding places: it is also evident in many *apparently* unpurposeful responses. As Loeb remarks (1918), the Aristotelian point of view still prevails in biology namely, that an animal only moves for a purpose, either in connection with those functions just enumerated, or in relation to something else connected with the preservation of the individual or the race. In the words of this writer, "Science began when Galileo overthrew the Aristotelian mode of thought and introduced the method of quantitative experiments which leads to mathematical laws free from the metaphysical conception of purpose. The analysis of animal conduct only becomes scientific in so far as it drops the question of purpose and reduces the reactions of animals to quantitative laws." While admitting the justice of Loeb's remarks, we do not consider it desirable to eliminate all question of purpose from work of this nature, as the habits of a particular species not infrequently suggest the application of substances of chemotropic value, improbable to come under notice, except fortuitously, in other ways. Nevertheless, in many instances, it is remarkably difficult to prove that the observed facts bear the relation to a particular function which at first sight appears evident. The use of baits to attract insects was known to agriculturists of a hundred years ago, and when our forefathers found their land to be infested by wire worms they adopted the plan of burying beneath the soil slices of potatoes impaled on skewers (Weiss, 1912). These were examined frequently and the larvae which were attracted were collected and destroyed. One of the first important contributions to the scientific study of chemotropism, with reference to insects, is the work of Barrows (1907) who investigated the reactions of the pomace fly to odorous substances. This insect occurs in great numbers around cider-presses, packing sheds, orchards and other

situations where fermenting fruit is present; within the latter it deposits its eggs and its larvae develop. Barrows investigated the reactions of this fly to the various chemical constituents of fermenting fruit. Ethyl alcohol, acetic ether and acetic and lactic acids were experimented with separately, and in mixture. The insect was found to be attracted in the most marked degree by a mixture of ethyl alcohol of 20 per cent. strength and acetic acid of 5 per cent. It was further discovered that cider vinegar and fermented cider contain alcohol and acetic acid in percentages very close to those just quoted. A series of experiments were conducted proving that the fly discovers its food by means of the olfactory sense, the latter being located in the terminal joint of the antennae. In 1908, Forbes experimented with various reagents with reference to the Corn Root Aphis, with the object of discovering substances towards which this species reacts negatively. The seeds were treated with various chemicals of which carbolic acid, formalin, kerosene and oil of lemon were found to be of value as repellants, aphis attacks being noticeably reduced after the seeds had been thus dealt with. In 1910 Verschaffelt published an important and highly suggestive paper, embodying his investigations of the factors which determine the selection of food in the case of the larvae of *Pieris brassicae* and *P. rapae*. The larvae select as their food plants certain Cruciferae, also *Tropaeolum* and *Reseda*. In these plants there occurs a group of glucosides—the mustard oils. Verschaffelt took a solution of sinigrin, which constitutes the glucose agent in black mustard, and uniformly distributed it over the leaves of plants which the *Pieris* larvae had previously refused to eat. Leaves so treated were devoured readily. From such experiments it appears that the *Pieris* larvae exhibit a marked chemotropism towards mustard oils, and it is due to their presence in the leaves of certain plants that determines the selection of the latter by the larvae for their food. By a similar method of research, Verschaffelt has shown that the larvae of the saw-fly, *Prionophorus* (*Cladius*) *padi*, which feed on certain of the Rosaceae, are attracted by the glucoside known as amygdaline. As regards those factors which determine the females to select certain species of plants for purposes of oviposition, definite information might be acquired by carrying out an analogous series of experiments. In 1911 Patterson observed that flies (Sarcophagidae) would not oviposit on freshly killed material (caterpillars) in the cages even though the females had been ovipositing previously on older decomposing caterpillars. This would tend to show that the material must reach a certain stage of decomposition before the female would oviposit. In 1912 Howlett published some

observations dealing with the reactions of certain Indian fruit flies. He found that citronella oil exercises a remarkable attraction for the males of *Dacus diversus* and *D. zonatus*, and suggested that possibly this reagent is allied to a secretion emitted by the females, and that the phenomenon of the only being attracted is to be regarded as a reproduction, by artificial means, of a sexual attraction similar in kind to that which operates in most cases of "assembling." In a later paper (1915), Howlett conducted a further series of experiments, confirming his previous results that certain odours are remarkably attractive to male flies of the genus *Dacus* and, that by the employment of attractive substances, the movements of the flies can to a great extent be controlled in any given direction. Three of the common species (*D. diversus*, *ferrugineus* and *zonatus*) normally breed respectively in (1) anthers of Cucurbitaceae, (2) fruits of Solanaceae and mango, and (3) peach, guava, mango and other fruits. *D. diversus* (1) is most strongly attracted by iso-eugenol, *zonatus* by methyl-eugenol, and *ferrugineus* (2) by both iso- and methyl-eugenol. The odours of these substances have not yet been identified with those of the plants which constitute the normal breeding-places, but male flies have been found attracted to mango, Papaya, a Cycad and *Colocasia*, plants with a very characteristic smell similar to that of eugenol-derivatives. Females have never been seen to frequent these plants or to breed in them, but more extended observation on this point is needed. Three explanations suggest themselves. (a) That the smell is a direct sexual guiding smell, emitted by the female as previously suggested, but the young crushed females do not attract males. (b) The smell is not emitted by the female, but may be termed an "indirect" sexual guide to the plants where the females are accustomed to congregate for breeding purposes. Under these circumstances it is difficult to see why females should not be attracted by the odoriferous chemicals. (c) The odour is a food smell; if this be so it can only be attractive to males. It is evident that further critical research is greatly needed eliminating, at any rate for the time being, the metaphysical conception of purpose. In a third paper Howlett (1914) noted the marked response of Thrips to the stimulus of the odours of benzaldehyde, cinnamylaldehyde and anisaldehyde. In his earlier paper (1912), Howlett conducted a further series of experiments with regard to the influence of reagents upon oviposition and it appears not unlikely that the odours of chemical substances provide the required stimulus. Thus, he found *Sarcophaga* to be very strongly attracted to a flask containing a solution of skatol, a substance normally present in faeces and many larvae were

deposited therein. *Stomoxys calcitrans* was also induced to oviposit on cotton wool soaked with valerianic acid—a substance occurring in decaying vegetable refuse. Howlett further adds that both valerianic and butyric acids have a similar attraction for an Ortalid fly of the genus *Ulidia* (?) in India. H. H. P. and H. C. Severin (1913–15, 1918) have made a series of studies on the attraction of kerosene for the Mediterranean fruit fly, *Ceratitis capitata*. Enormous numbers of this species have been trapped by the agency of kerosene in various parts of the world, but the number of females attracted is negligible. This species is also attracted by crude petroleum, naphtha distillate, gasolene, etc., all mineral oils that do not normally occur in the environment of the species. Chatterjee (1915) in India has discovered that kusum oil (oil from *Schleicheria trijuga*) has a marked attraction for both sexes of the Coreid bug *Serinetia augur* Fabr., and also for the nymphs in all stages. Dean (1915) has discussed the value of poisoned bran mash flavoured with orange or lemon juice and distributed over areas infested with grasshoppers, army worms, cut worms, etc. In each case the chemotropic value of the mixture was greatly enhanced by the addition of orange or lemon. According to Simpson (1918) tsetse flies are attracted by oil of cloves, essence of orange and essence of lemon. In Queensland, Jarvis (1916) has found that the cane beetle (*Lepidiota albobirta*) is not influenced by the oils of plants allied to its food plant, but is attracted by cajeput oil, acetic acid, carbolic acid, nitrobenzene, and especially oil of almonds. We have, therefore, numerous instances of responses towards substances which do not occur in the normal surroundings of an insect.

The chemotropic responses of the house-fly have been more extensively investigated than those of any other insect. Thus Morrill in 1914 conducted a series of experiments with a variety of substances some of them of great chemical complexity, and varying very much in their chemotropic properties. Among others vinegar and beer (under certain conditions) were both found to be markedly attractive; formalin varied exceedingly. Commercial alcohol (95 per cent.) 1 pint, and water 20 pints, was found to be more attractive after the addition of sugar. The addition of bread to alcohol and alcohol mixtures increased their attractive properties, and also those of various other substances. Commercial dried blood, moistened with water, was found to have an attractive value greater than fresh and decomposed meat and fish. Cane syrup, and sugar and water, were found to have relatively low attractive values when used without other materials. Buck (1915) conducted somewhat similar experiments and found that not less than 3 per cent. nor more than 8 per

cent. of 95 per cent. ethyl alcohol in water was a good attractive agent. Sucrose was found to be a valuable addition to various baits, sometimes increasing their attractive properties 10-20 per cent. According to Richardson (1916) the female house-fly is strongly attracted towards manure for purposes of oviposition, food being only a secondary object. He exposed a number of liquids and found that ammonium carbonate was the most attractive. Small amounts of water and carbon dioxide, both constituents of ammonium carbonate, were not sought after by the flies, and it was concluded that the other constituent, ammonia, was the real attracting agent. Of the flies attracted only 7.6 per cent. were males. His experiments indicated that manure which was liberating ammonia was more attractive than fresh manure. Richardson was successful in inducing oviposition on a mixture of moist Timothy chaff and ammonium carbonate, whereas the chaff alone produced no result. In experiments conducted with moist sterilised absorbent cotton, ammonium carbonate exercised practically no chemotropic stimulus for oviposition, but was effective when traces of butyric acid were added: valerianic acid was attractive to a lesser degree. Crumb and Lyon (1917) investigated the question more fully, and produced evidence suggesting that carbon dioxide is the chief stimulant for oviposition, giving an 82 per cent. higher stimulus than ammonia. Richardson (1916) conducted some further experiments with reference to the attraction of Diptera to ammonia and found that it attracted various species. Those which respond to this stimulus are known to spend at least part of their lives in some form of animal excrement. The response is not always a simple one as was shown in his earlier investigation. In this same paper Richardson remarks that he was unable to induce *Stomoxys calcitrans* to oviposit on cotton wool soaked in valerianic acid, although Howlett was successful with this experiment in India. In 1917 Richardson conducted a series of tests with reference to the house-fly, using a wide range of substances placed in fly traps. A number of carbohydrates were tested in solution and, on the whole, they did not prove very attractive: lactose attracted the largest number of flies and starch the least. Dextrin also caught a comparatively large number of flies, but sucrose was consistently a poor attractive agent. In using alcohols and acids he found that 4 per cent. amylic alcohol gave better results than ethyl alcohol. Ethyl alcohol in 4 per cent. strength was more attractive than in 10 per cent. concentration; 10 per cent. acetic acid gave better results than 4 per cent. Succinic and lactic acids exhibited some attractive qualities in two experiments. Maltose, lactose, sucrose and dextrin in 4 per cent. solutions of amylic alcohol, ethyl

alcohol and acetic acid were found more attractive than the aqueous solutions of these substances. Crude gluten from wheat flour was not attractive. The water soluble portion, with or without starch in suspension, was decidedly attractive. Several experiments with milk indicated that fat-free caseinogen is attractive while butter fat is not. In 1918 Miss Lodge published a paper on the sense-reactions of flies—mainly those species likely to be concerned with the spread of intestinal diseases. The experiments were conducted indoors, and the different substances were tested both upon free flies and those confined in glass cylinders provided with muslin tops. The authoress states that the most suitable medium for the experimental tests was found to be equal parts of casein, sugar and banana, to which a solution of the substance to be tested was added. In all cases, therefore, an extraordinarily complex chemotropic substance was utilised, to which was added various other chemical agents of varying complexity. The results showed that, although many of the substances attracted a certain number of Diptera present in the room, yet none were so attractive that all the flies went to them. Pyrethrum extract, added to the medium already described, proved very attractive to *Calliphora*, ammonia proved attractive to *Phormia azurea*, ammonia and honey to *Musca domestica*; the latter insect was also attracted by honey and methylene blue, 1 per cent. nicotine, ammonium carbonate, and other substances. The addition of an aqueous solution of skatol was attractive to *Calliphora* and *Scatophaga*; camphor attracted *Calliphora* and also honey, the latter substance was attractive also to *Lucilia caesar*. As a control the casein mixture was adopted and this substance proved more attractive to *Calliphora* and *Lucilia* than any other reagent when added to it. Mineral and tar oils proved to be powerful repellents, the essential oils were, on the whole, repellents. Davidson (1918) states that 12 per cent. glycerine and 5 per cent. sugar to which was added 1 per cent. sodium arsenite proved a successful poisonous attractive agent for flies during the Egyptian campaign of the late war. Parker (1918) found a combination of beer and oatmeal proved a most attractive substance for the females of various Diptera frequenting privy vaults in Montana.

In the foregoing summary of the literature bearing upon Chemotropism we have included the more important papers but it makes no pretence of being exhaustive. A further object of this resume is to emphasise the fact that no systematic quantitative work has yet been attempted, and most of the observations so far recorded concern particular species only. A large number of chemical substances are sufficiently volatile to merit adequate trials, and it is our intention during these

researches to examine as many as possible, recording the species which respond, irrespective of whether they are injurious or otherwise. We are of opinion that quantitative work of this kind will provide a broader basis for a scientific understanding of the problems involved, than specialised experiments conducted for the purpose of combating any particular species of injurious insect.

III. METHODS.

Experimental researches upon chemotropism divide themselves into two groups—those conducted under the more or less artificial conditions of an enclosed room, and those carried out under field conditions. It is scarcely necessary to add that preliminary experiments in any branch of physiology need to be carried out under definitely known and controllable conditions of temperature, light, humidity, air currents, etc., and in such a way as to eliminate as many of these factors as may be desired. Such simplified conditions are scarcely possible in researches of the nature under consideration, except in the case of experiments conducted indoors. Our present researches are entirely concerned with field experiments, and we are firmly of the opinion that preliminary indoor trials are of little value in this connection. Insects reared and liberated under artificial conditions, and surrounded by a totally alien environment, do not necessarily react in a manner similar to those living free in their natural habitat. In the case of insects concerned with the spread of disease, and normally frequenting dwellings, hospitals, etc., these remarks naturally do not apply, and their reactions form no part of our observations.

Chemotropic work in the field presents innumerable difficulties and in no line of biological research with which we are acquainted is there so large a number of environmental and other factors to be taken into consideration. Success or failure of any chemotropic experiment depends primarily upon the presence of favourable atmospheric conditions. One is therefore largely at the mercy of climatic influences, which, in a country like England, are extremely variable. Temperature, air-currents, humidity, etc. have a direct bearing upon the evaporation of the substances to be tested, and the dissemination of their odours. Furthermore, atmospheric changes influence the tropisms of insects to a marked degree. Degree of temperature and amount of sunshine affect their activities, a dull cloudy day may inhibit their movements very noticeably, a strong wind interferes with flight, and excess of moisture inhibits their activities in other directions. There are also many unknown factors which exercise

their influence in different ways: the time of day, season, degree of development of the gonads, age of the insects concerned, state of hunger, development of the eggs, whether oviposition is in progress or not, all probably have a definite bearing upon the chemotropic responses of insects, but we are totally in the dark as to how they manifest themselves. We have observed, and also Richardson (1917), that the same attractive substance may vary in effectiveness on different days under apparently similar atmospheric conditions. This may be due to one or other of the above-mentioned factors, or depend upon the actual number of insects present in a given locality at a particular time, or may in some way be correlated with sex attraction. Feytaud in his experiments in trapping moths discovered that some traps lured exceptionally large numbers, especially at the end of the season, and in some cases in the proportion of only two females to 54 males. He attributes this to sex attraction, females being trapped first, males subsequently following them. In view of the complexity of the factors which have to be taken into account, it is necessary to repeat every individual experiment a number of times during the season, and keep very full meteorological data. It will consequently be evident that reliable results, concerning the chemotropic properties of even a small number of substances, take several years to achieve.

All experiments to have any scientific value must be checked by a definite control. When a chemical agent is exposed, and it attracts certain insects, we acquire definite data. The question then to be gone into is its relative attractive value as compared with other substances. To prove that any substance exhibits attractive properties we are faced with a number of problems. The negative results do not necessarily imply that the agent has no attractive value, as the species which may respond to the stimulus may be absent from the immediate locality at a given time. It is, therefore, necessary to devise a double control—one to prove that certain species of insects are actually present at the place and time of observation, and the other to show that the substance being dealt with has, or has not, chemotropic properties. As mentioned above, water may serve as one control, but to devise the second control substance is less easy of achievement. It is necessary to use a substance known to exhibit powerful chemotropic properties and this, in itself, is liable to vitiate the experiment in attracting insects which might have otherwise responded to the substance required to be tested. The senses of insects are very acute, and minute traces of a reagent are known to produce marked results. We are also totally ignorant as to the distance

which the odour of a particular substance may exercise chemotropic properties. According to Howlett (1915) the radius of attraction of citronella oil for certain fruit flies may be taken as about half a mile: with many Lepidoptera the female probably attracts the male from a much greater distance. It is evident, therefore, we should guard against placing substances to be tested too near to each other. For every agent to be tested suitable controls have to be decided upon, and spaced as far apart as may be possible.

In our field experiments we have to obtain the following data:

- (1) Power of attraction of a substance in various dilutions and under varied atmospheric conditions.
- (2) Optimum attractive strength.
- (3) Relative powers of attraction as compared with other substances.
- (4) The species attracted, their numbers and the proportion of the sexes.
- (5) Meteorological data.

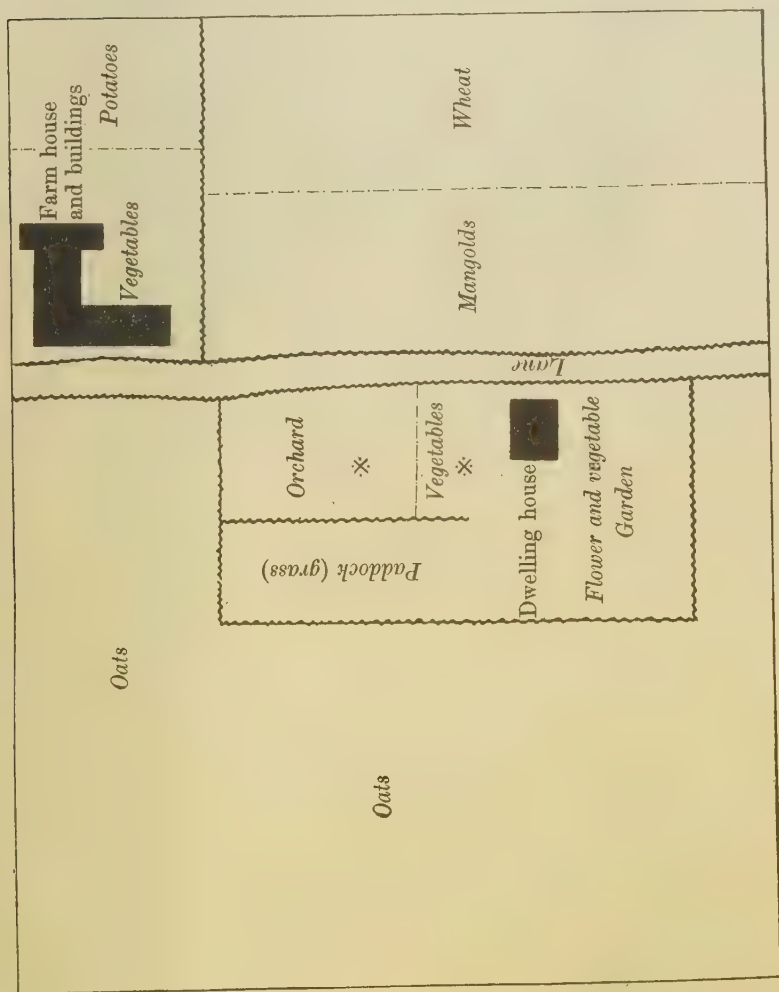
There are two methods of discovering substances likely to exhibit chemotropic attraction. The one is to undertake experiments with any substance that normally occurs in the environment of particular species, e.g. a constituent of the food of the larvae or adult, or likely substances chemically allied to the same. The second method is to test a large number of substances, necessarily somewhat indiscriminatingly at first, in the hope of discovering attractive agents. Verschaffelt (1910) observed that the alkaloid that gives mustard oil is the attractive agent in the larval food of *Pieris brassicae*; he started with the food plants and worked with the ingredients thereof. Richardson, who has studied the reactions of the house-fly to various agents, also followed this same method. He first observed that the house-fly is attracted to the manure heap by the odour of certain substances, which were being liberated during the early stages of fermentation. On this basis, he experimented with various inorganic and organic compounds that occur in the manure heap. This method is full of possibilities, in so far as individual species are concerned, but the second of the above methods has its advantages for preliminary quantitative work. It has been observed that a large number of insects are attracted towards chemicals that are neither associated with the smell of their food substances, nor occur in their normal environment. It is, moreover, in the discovery of such substances that some of the most striking results have so far been achieved. We have therefore followed this method of exposing a large number of chemicals and

recording the results. So far as possible we have worked with simpler substances, leaving the more complex organic compounds for later work. It is hoped that by this method it will be possible to discover whether any general relationship exists between chemical constitution and attractive properties.

The question of a suitable trap for exposing the agents used is of very great importance. It is essential that the substances to be tested should be exposed in traps so constructed as to admit any insects that are attracted thereto and, at the same time, preclude their escape. A free outlet for the uniform dispersal of the odour of each reagent used is essential and, furthermore, the constructional materials must be inodorous, and must not be readily acted upon by chemicals. Convenience of size and handling should not be overlooked, and the traps should be readily washable whenever necessary. After trials with various types of traps it was found that one based upon the Minnesota model (Washburn, 1912) was more suitable than any other. It possesses, however, the defect that insects can only enter around the base of the trap, and it is extremely likely that a certain number of insects which may be attracted do not succeed in entering. We have mainly used a rectangular trap of this type measuring $11'' \times 7'' \times 9''$ covered with ordinary fine white muslin, which can be readily renewed when necessary. The colour or condition of the trap appears to exercise some influence in the attraction of insects. Thus Dewitz (1912) states that white saucers are more attractive than coloured ones. Morrill (1914) also observed that insects came more readily to a new balloon trap than to a rusty trap. During trials conducted with clean empty traps, however, we found that the number of insects which entered therein was negligible. The greatest number was five Diptera and one Lepidopteron, after 36 hours exposure. In each experiment 50 c.c. of a chemical substance of a known strength was exposed for a given time, and full details recorded of any species attracted. It proved difficult during these preliminary trials to keep full meteorological data but, as far as possible, a record of maximum and minimum temperatures, both by means of ordinary and wet and dry bulb thermometers, was kept and the general conditions of the weather noted.

During one trial an empty trap was exposed on one occasion and we were surprised to find a considerable number of Diptera entrapped. On the previous day this same trap contained a markedly attractive agent and many insects were caught. It appears, therefore, evident that either the odour of the previous reagent lingers, and still exercises chemo-

tropic properties or, possibly, some smell is emitted by the flies themselves and their faeces, and serves to attract further individuals. The importance of using perfectly clean traps is thus rendered particularly important. The traps were suspended from trees and posts at a height of 2-4 feet from the ground. Owing to the junior author (Husain) having at his



~~~~~ Hedgrows of hawthorn.

\* Areas where experiments were conducted.

Fig. A. Somewhat diagrammatic sketch-plan showing the immediate surroundings of the areas where the experiments were conducted.

disposal the short period of only 10 weeks wherein to conduct these experiments, they can only be regarded as essentially preliminary in nature. War conditions also added to the difficulty in procuring certain reagents, and the summer of 1918 proved to be one of the wettest for a number of years. During the months of July–September there was scarcely more than two clear sunny weeks. Our observations were conducted at Lymm (Cheshire) in an orchard and vegetable garden, and the immediate surroundings are indicated in Fig. A. Less than 60 yards away are farm buildings and accompanying manure heaps which provide sustenance for great numbers of Diptera.

The length of exposure of a substance was generally 24–48 hours, but sometimes longer or shorter according to circumstances. Mr Husain, however, has not given very exact data upon this point. In all cases in which long exposures were resorted to, it was owing to adverse weather conditions which necessitated more lengthy trials.

As our observations are the first of their kind conducted in this country, we have deemed it advisable to publish them as they stand, without drawing any definite conclusions therefrom. We have laid particular stress upon the difficulties of the work, with a view of warning other intending observers of the pit-falls they are likely to encounter.

#### IV. OBSERVATIONS CONDUCTED AT LYMM (CHESHIRE) DURING JULY AND AUGUST, 1918.

(1) The following substances gave negative results, *i.e.* no insects were attracted, and it is probable that some of the agents used are powerful repellents.

|                                  |                            |  |                           |                             |
|----------------------------------|----------------------------|--|---------------------------|-----------------------------|
| Aqueous<br>solutions,<br>50 c.c. | Oil of cajeput             |  | }                         | Exposed on two occasions.   |
|                                  | ,, orange                  |  |                           |                             |
|                                  | ,, lemon                   |  |                           |                             |
|                                  | ,, sandal wood             |  |                           |                             |
|                                  | ,, bergamot                |  |                           |                             |
|                                  | ,, cloves                  |  |                           |                             |
|                                  | ,, juniper                 |  |                           |                             |
|                                  | Birch tar oil              |  | }                         | Exposed on three occasions. |
|                                  | Oil of aniseed             |  |                           |                             |
|                                  | ,, citronella              |  | Exposed on six occasions. |                             |
|                                  | Menthol                    |  | }                         | Exposed on two occasions.   |
|                                  | Turpeniol                  |  |                           |                             |
|                                  | { Potassium hydroxide (5%) |  |                           |                             |
|                                  | { Hydrochloric acid (5%)   |  |                           |                             |
|                                  | { Sulphuric acid (5%)      |  |                           |                             |
|                                  | { Malic acid (5%)          |  |                           |                             |
|                                  | { Benzaldehyde (5%)        |  |                           |                             |

All the oils enumerated above were used both in wire balloon traps and the Minnesota model traps. In one series of experiments a few drops were allowed to fall on blotting paper and placed in the usual receptacle within the traps. In a second series of experiments, an approximately similar quantity of each oil was added to 50 c.c. of water and shaken to form an emulsion.

(2) *Kerosene*. This substance is known abroad to attract insects belonging to such diverse groups as aphids, mosquitos, barklice, moths, cockroaches, Syrphid flies, Coccinellidae and their larvae, also a number of Tachinidae and parasitic Hymenoptera (Severin, H. H. P. and H. C., 1915). In our experiments it was exposed on four occasions: during one exposure it attracted a number of Nematocera, but on the remaining occasions the results were negative. It is important, however, to recognise that the kerosene used in these trials probably differed in composition from that employed in America.

(3) *Vinegar*. The records were as follows:

|             |                 |                |    |                               |
|-------------|-----------------|----------------|----|-------------------------------|
| Aug. 19-30. | 40 c.c. vinegar | 100 c.c. water | 22 | Diptera                       |
| Aug. 30-31. | 25 c.c. "       | 50 c.c. "      | 3  | "                             |
|             | 10 c.c. "       | 50 c.c. "      | 1  | " and 1 <i>Vespa vulgaris</i> |
|             | 5 c.c. "        | 50 c.c. "      | 2  | "                             |
| Aug. 31.    | 40 c.c. "       | 100 c.c. "     | 5  | "                             |

(4) *Ethyl alcohol*. Ethyl alcohol (approximately 95 per cent. strength) was used in the following percentages, 36, 22.5, 12.5, 10, 7, 5, 3, 2.5, 1, .7, .4, and .2. These solutions (50 c.c.) were used both as controls for other experiments and as independent chemotropic agents, but no attractive properties were evident in any instance. Our experiments with solutions stronger than 36 per cent. were vitiated, and need to be repeated. The 5 per cent. solution attracted eight Diptera and this result was only achieved after 48 hours exposure. Our results are somewhat remarkable in view of the fact that Richardson (1917), in New Jersey, caught 891 examples of *Musca domestica* in the course of six experiments, representing an aggregate of 207 hours exposure, using 4 per cent. ethyl alcohol. This observer found that a 10 per cent. solution, exposed in the same series of experiments, attracted 544 examples of that same species, which made up more than 95 per cent. of the Diptera attracted during the whole course of his trials. The latter were conducted within 50 yards of a prolific breeding ground of the insect, and our own experiments were carried out within 60 yards of farm accumulations of manure, and decaying organic matter of various kinds. Buck (1915), also in America, observed that not less than 3 per cent. and not more than 8 per cent. of 95 per cent. ethyl alcohol was a markedly attractive agent.

(5) *Glacial acetic acid*. Glacial acetic acid was not observed to exercise any marked chemotropic attraction as the following experiments indicate.

|             |               |         |                          |   |           |
|-------------|---------------|---------|--------------------------|---|-----------|
| Aug. 27-29. | 50 c.c. water | 5       | c.c. glacial acetic acid | 1 | Dipteron  |
| " 21-23.    | " "           | 1       | c.c. "                   | " | Nil       |
| " 21-22.    | " "           | .5 c.c. | " "                      | " | 3 Diptera |
| " 24-27.    | " "           | .5 c.c. | " "                      | " | 13 "      |
| " 27-29.    | " "           | .5 c.c. | " "                      | " | 12 "      |
| " 24-27.    | " "           | .1 c.c. | " "                      | " | 2 "       |

(6) *Ethyl alcohol and glacial acetic acid*. Unlike either of these substances, when used separately, a mixture of the two was found to be markedly attractive. Ethyl alcohol and acetic acid when brought into contact form small quantities of ethyl acetate and, as shown in Barrow's experiments (1907), ethyl acetate exercises a marked attraction for *Drosophila ampelophila*. The amount of ethyl acetate formed by using such small quantities of the two substances as 1 per cent. of ethyl alcohol and 0.05 c.c. of acetic acid under outdoor conditions must be very small. In each experiment 50 c.c. of ethyl alcohol or water was used.

|         |             |                        |                          |     |           |
|---------|-------------|------------------------|--------------------------|-----|-----------|
| Exp. 1. | Aug. 19-21. | 10% ethyl alcohol + 1  | c.c. glacial acetic acid | 69  | Diptera   |
| " "     | " "         | 10% "                  | " "                      | 0   | (control) |
| " 2.    | " 21-23.    | 10% " + 1              | c.c. "                   | 329 | Diptera   |
| " "     | " "         | water + 1              | c.c. "                   | 0   | (control) |
| " 3.    | " 21-22.    | 10% ethyl alcohol + .5 | c.c. "                   | 82  | Diptera   |
| " "     | " "         | water + .5             | c.c. "                   | 3   | "         |
| " "     | " "         | " "                    | " "                      |     | (control) |
| " 4.    | " 22-23.    | 10% ethyl alcohol + .5 | c.c. "                   | 12  | Diptera   |
| " "     | " "         | 10% "                  | " "                      | 2   | "         |
| " "     | " "         | " "                    | " "                      |     | (control) |
| " 5.    | " "         | 5% " + .5              | c.c. "                   | 41  | Diptera   |
| " "     | " "         | 5% "                   | " "                      | 2   | "         |
| " "     | " "         | " "                    | " "                      |     | (control) |
| " 6.    | " 27-29.    | 5% " + .5              | c.c. "                   | 214 | Diptera   |
| " "     | " "         | 5% "                   | " "                      | 8   | "         |
| " "     | " "         | " "                    | " "                      |     | (control) |
| " 7.    | " 22-23.    | 5% " + .2              | c.c. "                   | 14  | Diptera   |
| " 8.    | " "         | 5% " + .1              | c.c. "                   | 7   | "         |
| " 9.    | " 23-24.    | 5% " + .05             | c.c. "                   | 10  | "         |
| " 10.   | " "         | 2.5% " + .5            | c.c. "                   | 25  | "         |
| " 11.   | " "         | 2.5% " + .1            | c.c. "                   | 12  | "         |
| " 12.   | " "         | 2.5% " + .05           | c.c. "                   | 4   | "         |
| " 12a.  | " "         | 2.5% "                 | " "                      | 1   | "         |
| " "     | " "         | " "                    | " "                      |     | (control) |
| " 13.   | " 24-27.    | 1% " + .5              | c.c. "                   | 122 | Diptera   |
| " 15.   | " "         | 1% " + .05             | c.c. "                   | 45  | "         |
| " 15a.  | " "         | 1% "                   | " "                      | 0   | (control) |
| " 14.   | " "         | 1% " + .1              | c.c. "                   | 19  | Diptera   |
| " 14a.  | " "         | water + .1             | c.c. "                   | 2   | "         |
| " "     | " "         | " "                    | " "                      |     | (control) |

It appears evident, therefore, that the greatest attractive properties are exercised when at least .5 c.c. acetic acid is present, and they are enhanced by an increased strength of the alcohol. Experiments with greater strengths than 10 per cent. ethyl alcohol were unable to be carried out, owing to adverse weather conditions.

|        |     | Experiment nos. |    |     |    |    |    |    |    |    |     |    |     |     |     |                                   |  |  |
|--------|-----|-----------------|----|-----|----|----|----|----|----|----|-----|----|-----|-----|-----|-----------------------------------|--|--|
| Totals | 2   | 3               | 4  | 6   | 7  | 8  | 9  | 10 | 11 | 12 | 13  | 14 | 15  | 16  | 17  |                                   |  |  |
| 183    | 123 | 1               | —  | 18  | 1  | —  | —  | —  | —  | —  | 2   | —  | —   | 8   | 30  |                                   |  |  |
| 4*     | —   | —               | —  | —   | —  | —  | —  | —  | —  | —  | —   | —  | —   | 2*  | 2*  | <i>Rhyphus punctatus</i>          |  |  |
| 65     | 42  | 1               | —  | 7   | 1  | 1  | —  | —  | —  | —  | —   | —  | —   | 4   | 9   |                                   |  |  |
| 1*     | —   | 1*              | —  | —   | —  | —  | —  | —  | —  | —  | —   | —  | —   | —   | —   | <i>Rhyphus fenestralis</i>        |  |  |
| 1      | —   | —               | —  | —   | —  | —  | —  | —  | —  | —  | —   | —  | —   | —   | 1   |                                   |  |  |
| 25     | 7   | 5               | —  | 4   | —  | —  | —  | —  | —  | —  | 1   | —  | 1   | —   | 7   | <i>Onesia sepulchralis</i>        |  |  |
| 34     | 4   | 2               | —  | 4   | —  | —  | —  | —  | 1  | —  | 4   | 1  | —   | —   | 18  |                                   |  |  |
| 47     | 11  | 10              | 3  | 3   | —  | —  | 1  | 1  | —  | —  | 4   | —  | 1   | 1   | 12  | <i>Sarcophaga carnaria</i>        |  |  |
| 18     | —   | 4               | —  | 1   | —  | —  | —  | 1  | 1  | —  | 2   | —  | —   | 1   | 8   |                                   |  |  |
| 8      | —   | —               | —  | 2   | —  | —  | —  | —  | —  | —  | 1   | —  | —   | 1   | 4   | <i>Pollenia rudis</i>             |  |  |
| 1*     | —   | —               | —  | —   | —  | —  | —  | —  | —  | —  | —   | —  | 1*  | —   | —   |                                   |  |  |
| 6      | —   | —               | —  | 1   | —  | —  | —  | —  | —  | —  | 1   | —  | —   | —   | 4   |                                   |  |  |
| 3      | —   | —               | —  | 2   | —  | —  | —  | —  | —  | —  | —   | —  | 1   | —   | —   | <i>Graphomyia maculata</i>        |  |  |
| 1      | —   | —               | —  | 1   | —  | —  | —  | —  | —  | —  | —   | —  | —   | —   | —   |                                   |  |  |
| 17     | 4   | 2               | —  | 6   | 1  | —  | —  | —  | —  | —  | —   | —  | —   | —   | 4   | <i>Muscina stabulans</i>          |  |  |
| 10     | 2   | 2               | —  | 2   | —  | —  | —  | —  | —  | —  | —   | —  | —   | —   | 4   |                                   |  |  |
| 5      | 2   | —               | —  | —   | —  | —  | —  | —  | —  | —  | —   | —  | —   | 3   | —   | <i>Muscina caesia</i>             |  |  |
| 1      | 1   | —               | —  | —   | —  | —  | —  | —  | —  | —  | —   | —  | —   | —   | —   |                                   |  |  |
| 6      | 2   | 1               | —  | 1   | —  | —  | —  | —  | —  | —  | —   | —  | 1   | —   | 1   | <i>Muscina pabulorum</i>          |  |  |
| 8      | 4   | —               | —  | 2   | —  | —  | —  | —  | —  | —  | —   | —  | —   | —   | 2   |                                   |  |  |
| 16     | —   | 4               | 1  | 5   | —  | —  | 1  | —  | 1  | 1  | 2   | —  | —   | —   | 1   | <i>Mesembrina meridiana</i>       |  |  |
| 3      | —   | —               | —  | —   | —  | —  | —  | —  | —  | —  | 1   | —  | —   | —   | —   |                                   |  |  |
| 71     | 12  | 3               | —  | 14  | —  | —  | —  | 3  | 1  | —  | 6   | 1  | 1   | 10  | 20  | <i>Calliphora erythrocephala</i>  |  |  |
| 44     | 6   | 2               | —  | 14  | —  | —  | 3  | —  | —  | —  | 3   | —  | 1   | 7   | 8   |                                   |  |  |
| 56     | 9   | 3               | —  | 17  | —  | —  | —  | —  | —  | —  | —   | 1  | 3   | 2   | 21  | <i>Calliphora vomitoria</i>       |  |  |
| 64     | 7   | 1               | —  | 16  | —  | —  | —  | 1  | —  | —  | —   | —  | 3   | 2   | 30  |                                   |  |  |
| 75     | 19  | 6               | —  | 16  | —  | —  | —  | —  | —  | —  | 1   | 1  | 2   | 8   | 22  | <i>Lucilia sp.</i>                |  |  |
| 61     | 19  | 3               | —  | 14  | —  | —  | —  | —  | —  | —  | 2   | 1  | —   | 4   | 18  |                                   |  |  |
| —      | —   | —               | —  | —   | —  | —  | —  | —  | —  | —  | —   | —  | —   | —   | —   |                                   |  |  |
| 18     | 1   | 2               | —  | 1   | —  | —  | 2  | 2  | —  | —  | 3   | —  | —   | 2   | 5   | <i>Mydaea impunctata</i>          |  |  |
| 4      | —   | —               | —  | 1   | —  | —  | —  | —  | —  | —  | —   | —  | —   | —   | 3   | <i>Spilogaster duplicata</i>      |  |  |
| 5      | —   | —               | —  | 1   | —  | —  | —  | —  | —  | —  | —   | —  | —   | —   | 4   |                                   |  |  |
| 1      | —   | —               | —  | 1   | —  | —  | —  | —  | —  | —  | —   | —  | —   | —   | —   | <i>Hydrotaea dentipes</i>         |  |  |
| —      | —   | —               | —  | —   | —  | —  | —  | —  | —  | —  | —   | —  | —   | —   | —   |                                   |  |  |
| 110    | 4   | 4               | 1  | 15  | 4  | —  | 2  | 3  | —  | —  | 14  | 3  | 3   | 25  | 32  | <i>Hylemyia strigosa</i>          |  |  |
| 243    | 6   | 6               | 5  | 24  | 7  | 4  | —  | 14 | 7  | 3  | 36  | 9  | 11  | 53  | 58  |                                   |  |  |
| 2      | 1   | —               | —  | —   | —  | —  | —  | —  | —  | —  | 1   | —  | —   | —   | —   | <i>Hytodesia errans</i>           |  |  |
| —      | —   | —               | —  | —   | —  | —  | —  | —  | —  | —  | —   | —  | —   | —   | —   |                                   |  |  |
| 1      | 1   | —               | —  | —   | —  | —  | —  | —  | —  | —  | —   | —  | —   | —   | —   | <i>Anthomyia pluvialis</i>        |  |  |
| 2      | 1   | —               | —  | —   | —  | —  | —  | —  | —  | —  | —   | —  | —   | —   | 1   |                                   |  |  |
| 24     | 6   | 2               | 1  | 2   | —  | —  | —  | —  | —  | —  | 2   | 1  | —   | —   | 10  | <i>Fannia canalicularis</i>       |  |  |
| 1      | 1   | —               | —  | —   | —  | —  | —  | —  | —  | —  | —   | —  | —   | —   | —   |                                   |  |  |
| 6      | —   | 1               | —  | 1   | —  | —  | —  | —  | —  | —  | 1   | —  | 1   | 1   | 1   | <i>Scatophaga stercoraria</i>     |  |  |
| 5      | —   | —               | —  | 1   | —  | —  | —  | —  | —  | —  | —   | —  | —   | 1   | 3   |                                   |  |  |
| 208*   | 34* | 14*             | 2* | 17* | —  | 2* | 1* | —  | 1  | —  | 30* | 1* | 15* | 69* | 22* | Unidentified, mostly Anthomyiidae |  |  |
| 1466   | 329 | 82              | 13 | 214 | 14 | 7  | 10 | 25 | 12 | 4  | 121 | 19 | 45  | 204 | 365 | Totals                            |  |  |

Unidentified,  
mostly  
Anthomyidae

On Aug. 24-29 (Exp. 17) two vessels were placed closely together in the same trap: one contained 50 c.c. of 5 per cent. ethyl alcohol, and the other 50 c.c. of 1 per cent. glacial acetic acid. The vapours of the two solutions coming in contact would produce very minute quantities of ethyl acetate. This, however, proved to possess powerful attractive properties, 365 Diptera pertaining to various species being entrapped. In another experiment (No. 16) (Aug. 24-27), 50 c.c. 2 per cent. glacial acetic acid was used, and the same quantity of 10 per cent. ethyl alcohol was placed in a second vessel as before, and 204 Diptera were attracted during 42 hours exposure. The question arises whether it is the vapour of the ethyl acetate that is alone responsible for this attraction, or the mixed vapours of the ethyl alcohol, acetic acid and ethyl acetate that produced the effect. This problem is at present unanswered. As a control on the same days (Aug. 27-29) 5 per cent. ethyl alcohol attracted only eight Diptera.

An analysis of the species attracted and the number of each sex obtained is given on p. 285. The numbers at the head of each column refer to those allotted to each of the foregoing experiments. The figures opposite each species refer to the number of individuals attracted, the upper figures representing males and the lower figures females: figures bearing \* are cases in which the sexes of the individuals were not determined.

7. *Ethyl acetate*. We have so far only conducted a few experiments with this ester. From Aug. 2-8 an emulsion of 10 c.c. of ethyl acetate in 50 c.c. of water attracted only 39 Diptera. From Aug. 8-12 a mixture of 5 c.c. ethyl acetate and 50 c.c. of a 25 per cent. solution of cane molasses proved attractive. During the same period a trap containing 25 c.c. of beer in place of the ethyl acetate attracted 108 examples of various Diptera.

8. *Methyl acetate*.

Aug. 12-14. 5 c.c. water + 10 c.c. methyl acetate. 3 Diptera.

„ 15-16. 5 c.c. 10% ethyl alcohol + a few drops of methyl acetate. 11 Diptera.

9. *Amylic acetate*. On Aug. 16-19 an emulsion consisting of 33 per cent. amylic acetate in water attracted seven Diptera: with 20 per cent. amylic acetate six Diptera were attracted, and with 9 per cent. acetate 10 Diptera responded.

(10) *Butyric and valerianic acids*. Normal butyric acid in water exhibited no attractive properties, but traces of this substance in ethyl alcohol proved very attractive, this property probably being due to the ethyl butyrate formed. Iso-butyric acid gave less satisfactory results.

Traces of valerianic acid in ethyl alcohol is also an attractive mixture. The experiments were as follows:

|    |             |                   |                             |    |         |
|----|-------------|-------------------|-----------------------------|----|---------|
| 1. | Aug. 15-16. | 10% ethyl alcohol | + traces of butyric acid    | 39 | Diptera |
|    | " 16-19.    | Water             | + " " "                     | 3  | "       |
| 2. | " 21-22.    | 10% ethyl alcohol | + .5 c.c. butyric acid      | 82 | "       |
|    | " "         | Water             | + .5 c.c. " "               | 2  | "       |
| 3. | " 22-24.    | 10% ethyl alcohol | + .5 c.c. " "               | 20 | "       |
| 4. | " "         | 10% "             | + .5 c.c. iso-butyric acid  | 7  | "       |
|    | " "         | 10% "             | — — —                       | 2  | "       |
| 5. | " 15-16.    | 10% "             | + traces of valerianic acid | 37 | "       |

The species attracted were as follows: an \* indicates that the sex was undetermined.

| Exp. 1 | Exp. 2 | Exp. 5 | Species attracted                  |
|--------|--------|--------|------------------------------------|
| 1 ♂    | 2 ♂    | —      | <i>Sarcophaga carnaria</i>         |
| —      | 1 ♀    | —      | <i>Pollenia rudis</i>              |
| 1 ♂    | —      | —      | <i>Musca domestica</i>             |
| 1 ♂    | 2 ♂    | —      | } <i>Calliphora erythrocephala</i> |
| 1 ♀    | —      | —      |                                    |
| —      | 3 ♂    | —      | <i>C. vomitoria</i>                |
| —      | —      | 1 ♂    | <i>Mesembrina meridiana</i>        |
| 3 ♀    | 2 ♀    | 1 ♀    | <i>Mydaea impuncta</i>             |
| —      | —      | 1 ♀    | <i>Spilogaster duplicata</i>       |
| 1 ♀    | 2 ♀    | —      | <i>Muscina stabulans</i>           |
| —      | 1 ♂    | —      | } <i>M. caesia</i>                 |
| —      | 1 ♀    | —      |                                    |
| —      | —      | 1 ♂    | } <i>M. pascuorum</i>              |
| —      | 1 ♀    | —      |                                    |
| 10 ♂   | —      | 5 ♂    | } <i>Hylemyia strigosa</i>         |
| 13 ♀   | 2 ♀    | 8 ♀    |                                    |
| 4 ♂    | 1 ♂    | 1 ♂    | <i>Fannia canalicularis</i>        |
| 4*     | 64*    | 19*    | Unidentified, mostly Anthomyidae   |
| 39     | 82     | 37     | Totals                             |

(11) *Beer*. Beer has long been known to exercise marked chemotropic properties. It forms an important constituent of a number of baits used on a practical scale, for the purpose of attracting and trapping injurious Lepidoptera. Our observations confirm the high attractive properties of this substance, and we have also been able to definitely prove that it is equally, or even more, attractive in so far as Diptera are concerned. Beer is a complex chemical substance, whose composition varies in almost every sample, and it is essential to ascertain which constituent or constituents exercises this power. Our researches are now being conducted with this object in view.

The following experiments were performed for the purpose of testing the relative value of 50 per cent. solutions of beer and a mixture of beer

and cane molasses—the latter itself being an important attractive agent. Two small American balloon traps were fitted up for the purpose and were suspended close together from the same tree. The one trap A was charged with 60 c.c. beer solution and the other trap B was charged with 30 c.c. undiluted beer and 30 c.c. of a 25 per cent. solution of cane molasses, with the following results. July 13–14. Trap A, 11 flies; B, 11 flies. July 14–16. A, 4 flies; B, 57 flies. July 16–19. A, 5 flies; B, 65 flies. It was observed that Diptera responded much more quickly to the stimulus of beer, but the latter speedily lost its attractive properties. After the second day, probably on account of the fermentation which was going on in the molasses mixture, trap B became far more attractive. On July 6–8, 200 c.c. of a 50 per cent. solution of beer in a Minnesota trap attracted 928 Diptera, the largest number recorded in any of our experiments. On July 11–13 a 33 per cent. solution of beer attracted 175 Diptera. The species attracted are recorded below, the figures in brackets referring to the weaker solution. *Scatopse* sp. 11\*. *Rhyphus punctatus* Fab. 98♂, 60♀, 27\* (5♂, 2♀). *R. fenestralis* Scop. 2♀. *Onesia sepulchralis* L. 20♂, 12♀ (4♂, 6♀). *Sarcophaga carnaria* L. 2♂, 6♀ (5♂, 1♀). *Pollenia rudis* Fab. 8♂ (2♂, 5♀). *Muscina stabulans* Fall. 1♂. *Morellia hortorum* Fall. 1♂, 1♀. *Mesembrina meridiana* L. 8♂, 3♀ (2♂). *Pyrellia eriophthalma* Macq. 8♂, 10♀ (1♀). *Calliphora erythrocephala* Mg. 29♂, 24♀ (3♂). *C. vomitoria* L. 6♂, 3♀ (1♀). *Euphoria* sp. 1♀. *Lucilia* sp. 12♂, 8♀. *Mydaea meditabunda* F. 4♂, 1♀ (1♂, 2♀). *M. impuncta* Fall. 23♂, 11♀ (6♂). *Spilogaster duplicata* Mg. 3♀. *S. pubescens* Stein. 3♂. *S. demigrans* Ztt. (1♂). *Hydrotaea dentipes* Fab. 7♂, 1♀ (1\*). *Hylemyia strigosa* Fab. 92♂, 30♀ (37♂, 44♀). *Poliates lardaria* Fab. 3♂, 8♀ (1♂). *Hytodesia marmorata* Ztt. 2♀. *Anthomyia pluvialis* L. 1♀. *Fannia canalicularis* L. 7♂ (2♂). *F. manicata* Mg. 1♂. *Fannia* sp. 17♂, 5\*. *Scatophaga stercoraria* L. 16♂, 2♀ (5♂, 10♀). *Themira putris* L. 1♂. *T. minor* Hal. 1♂, 7♀. *Drosophila obscura* Fall. 2\*. *Dolichopus griseipennis* Stan., *Piophilus vulgaris*, *P. nigriceps* Mg., a few examples of each were attracted by the 50 per cent. solution and many examples of a species of *Sciara* and *Sepsis*. *Helomyza* sp., a few examples were attracted by both solutions. Unidentified Diptera (mostly Anthomyiidae) 300 (32).

(12) *Cane molasses*. The variety used was that commonly known as "black treacle"—an extremely complex substance of variable chemical composition. Our researches have not so far included an investigation of the attractive agents present, but it is intended to pursue this line of research at the earliest opportunity. Cane molasses (50 c.c.) was used

in 25 per cent. and 50 per cent. solutions in distilled water, both alone, and with the addition of certain other substances as detailed below.

|            |              |     |           |         |               |     |         |
|------------|--------------|-----|-----------|---------|---------------|-----|---------|
| July 4- 5. | 50% solution | ... | ...       | ...     | ...           | 256 | Diptera |
| " 8-12.    | 25% "        | ... | ...       | ...     | ...           | 36  | "       |
| " "        | 25% "        | +   | (50 c.c.) | 25 c.c. | beer          | 108 | "       |
| " "        | 25% "        | +   | 5 c.c.    | 10%     | ammonia       | 8   | "       |
| " "        | 25% "        | +   | 5 c.c.    | 10%     | malic acid    | 12  | "       |
| " "        | 25% "        | +   | 5 c.c.    | 5%      | acetic acid   | 4   | "       |
| " "        | 25% "        | +   | 5 c.c.    |         | ethyl acetate | 2   | "       |

It is evident from these results that cane molasses in strong solution is an extremely attractive substance. When used in 25 per cent. solution its chemotropic properties are increased by the addition of beer, but in these experiments the addition of the other substances quoted above had no positive effect.

*Species attracted*.—50 per cent. solution. *Rhyphus punctatus* Fab. 48♂, 21♀. *Onesia sepulchralis* L. 15♂, 8♀. *Sarcophaga carnaria* L. 2♂. *Pollenia rudis* Fab. 5♂, 4♀. *Muscina* (*Cyrtoneura*) *stabulans* Fall. 1♂, 1♀. *M. pabulorum* Fall. 3♀. *Morellia hortorum* Fall. 1♂. *Pyrellia eriophthalma* Macq. 1♂, 4♀. *Phormia* sp. 1♂. *Calliphora erythrocephala* Mg. 3♂, 1♀. *Mydaea mediatubunda* F. 2♂, 2♀. *M. impuncta* Fall. 11♂. *Spilogaster duplicata* Mg. 5♂. *S. pubescens* Stein. 1♂. *Hydrotæa dentipes* Fab. 2♂, 2♀. *Hylemyia strigosa* Fab. 29♂, 13♀. *Poliætes lardaria* Fab. 5♂, 7♀. *Hyttodesia errans* Mg. 1♂. *Chortophila trichodactyla* Rond. 1♂. *Fannia* sp. 11♂, 9♀. *Scatophaga stercoraria* L. 2♂, 1♀. *Helomyza* sp., *Themira putris* L., *T. minor* Hal., *Sepsis* sp., *Sciara* sp., a few examples of each. Unidentified Diptera, mostly Anthomyiidae 30.

25 per cent. solution + 25 c.c. beer.—*Rhyphus punctatus* Fab. 21♂, 12♀, 2 sex not determined. *Onesia sepulchralis* L. 5♂. *Sarcophaga carnaria* L. 1♂, 1♀. *Pollenia rudis* Fab. 1♂. *Muscina stabulans* Fall. 1♂, 1♀. *Calliphora erythrocephala* Mg. 21♂, 12♀. *C. vomitoria* L. 2♂, 1♀. *Euphoria* sp. 1♀. *Lucilia* sp. 16♂, 7♀. *Poliætes lardaria* Fab. 1♂. *Hyttodesia errans* Mg. 1♀. *Anthomyia pluvialis* L. 1♂, 1♀. *Themira putris* L., *T. minor*, *Sepsis* sp., *Sciara* sp., a few examples.

We do not regard it likely to be of much value, at present, to publish the meteorological records kept in these preliminary experiments. The trials were not conducted on a sufficiently extensive scale to warrant any conclusions being drawn, with reference to the relations between weather conditions and insect behaviour. Furthermore, owing to the war we were unable to procure the necessary self-recording instruments. Without the aid of the latter, the data provided by the ordinary wet and dry

bulb thermometer, for example, are of little comparative value, and could not be obtained during the night. The most noteworthy features of the experiments enumerated in the preceding pages may be summarised as follows.

1. The experiments were conducted during July and August 1918, and for the most part during wet and apparently unfavourable climatic conditions.

2. The insects attracted consisted almost exclusively of Diptera. With the exception of one or two examples of *Vespa vulgaris*, no Hymenoptera responded. Rhynchota, Coleoptera and Neuroptera (*sen. lat.*) were unrepresented. A small number of Noctuid Lepidoptera entered the traps, but for the purpose of conducting experiments with such relatively large insects, as many Lepidoptera, it would be necessary to slightly alter the construction of the traps used in order to allow of greater facilities for ingress.

3. Beer, cane molasses, and mixtures of these two substances are powerful chemotropic agents for various Diptera. Ethyl alcohol, in various concentrations, exhibited little or no chemotropic properties but with the addition of small amounts of butyric, valerianic or acetic acids it exercised a powerful stimulus. Aqueous solutions of the above acids were not attractive, the respective esters probably being the attractive agents in each case. The remaining substances utilised in these experiments were found to exhibit little or no positive chemotropic properties.

4. Out of considerably over 3000 Diptera attracted during the course of these observations, by far the greater number pertained to one or other of the five families Rhyphidae, Mycetophilidae, Sepsidae, Muscidae and Anthomyidae.

5. As a general rule members of both sexes of a species were attracted irrespective of the chemotropic agent employed. In the majority of instances males predominated over females, but in no case where the number of individuals of a species attracted exceeded 20 was the disproportion greater than 2.9 males to 1 female.

6. *Rhyphus punctatus*, *Hylemyia strigosa* and *Calliphora erythrocephala* were the dominant species attracted.

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ON FORMS OF THE HOP (*HUMULUS LUPULUS* L. AND *H. AMERICANUS* NUTT.) RESISTANT TO MILDEW (*SPHAEROTHECA HUMULI* (DC.) BURR.).

IV.

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IN previous articles<sup>(1)(2)(3)</sup> it has been pointed out that resistance to the attacks of the mildew *Sphaerotheca Humuli* (DC.) Burr. is found in certain forms of *Humulus Lupulus* L., viz., (1) in a variety known to nurserymen as the "Golden Hop," and (2) in certain seedlings of the wild plant obtained from Italy. Experiments have now demonstrated the existence of a form of *H. americanus* Nutt. resistant to mildew. Our present knowledge with respect to these three groups of mildew-resistant hops is given below.

(1) THE "GOLDEN HOP."

Several distinct forms of *H. Lupulus* with yellow ("golden") leaves are on sale by nurserymen. These forms are quite distinct, and in several instances the stocks in nurseries have become mixed. The following information has been collected with respect to the characteristics, origin and name of these forms.

(1) Plants were obtained under the name of "Golden Hop" from Messrs Bunyard and from Messrs Bide and Son. In both cases the stock proved to be mixed, the plant sent being sometimes female and immune, and sometimes male and fully susceptible to mildew. Mr E. A. Bunyard has written to me: "I fancy our 'Golden Hop' came from Messrs Bide and Son, but no record was kept." Messrs Bide and Son wrote, in March, 1916: "We bought the plants in the first place from M. G. Bénard, Orleans, France. We do not claim to be the introducers of this plant, as we quite think it is to be had from other firms in this country." In Feb. 1918, Mr A. R. Bide wrote: "I cannot tell you definitely how many years we have listed this, but it is certainly 8 to 10. I first saw this growing in the nursery of Messrs Turbat et Cie, when I was at Orleans, and as I had never seen the Golden variety before, I bought some. Since

then we have worked a stock of our own." In answer to enquiries, M. Bénard wrote: "La variété *Humulus Lupulus aureus* m'a été fournie d'après ce que je crois me rappeler par M. Heerma Van Voss, pépiniériste à Oudenbosch (Hollande), ce qui explique que je n'en suis pas l'obteneur"; and Messrs H. W. van der Bom and Co. (U. J. Heerma Van Voss) wrote: "our Mr Heerma has not introduced the Golden Hop (*H. Lupulus* var. *aureus*).". Messrs E. Turbat et Cie wrote: "We are not the originators of it."

It seems clear from the above information that one stock of the "Golden Hop" was imported from the Continent, and we may perhaps assume that it was at the time mixed, and consisted of an immune female plant—as to the origin of which I have not up to the present been able to obtain any information—and a susceptible male plant, which, as will now be shown, is probably to be identified as the *H. Lupulus aureus* described from Germany.

(2) Another stock of the "Golden Hop" in this country has been distributed from Messrs Dicksons, who very kindly supplied me with plants in 1917. With regard to the origin of this plant the firm wrote: "*H. Lupulus aureus* originated from a sport about 1893. It was discovered in a botanic garden in Germany and we bought half the stock which is very limited. We propagated and sent out 3 years afterwards (1896). It is propagated from shoot and root cuttings. The book containing the record has been destroyed. We issued a coloured plate of it, but the supply is now exhausted. This plate does not show the sex of the plant. We have so far as we know only the female form."

All the plants sent by Messrs Dicksons proved (in the greenhouse) to be susceptible to mildew, and those which flowered the next year in the hop garden (being the same individuals as those which were susceptible to mildew the previous year) all proved to be males. On acquainting Messrs Dicksons with the latter fact, the firm wrote: "Several of our Golden Hops are flowering this year but all are male plants."

Through help given by Prof. L. H. Bailey, it became possible to identify this male "Golden Hop" obtained from Germany. Prof. Bailey referred me to *Die Gartenwelt*, III, 1899, p. 476, from which I transcribe below the more important descriptive parts: "Neue Pflanzen. *Humulus Lupulus aureus* Von C. Bonstedt, Obergärtner des botanischen Gartens in Rostock....Als neuestes Goldkind, welches sich den Genannten ebenbürtig zur Seite stellt, führe ich heute den geschätzten Lesern eine Schlingpflanze und zwar einen Sport des allbekannten Hopfens (*H. Lupulus* L.) vor....*H. Lupulus aureus* ist bis jetzt nur in männlichen Pflanzen

vorhanden....Aufgefunden wurde diese hübsche Form vor etwa zehn Jahren von Baumschulbesitzer Finck aus Doberan, der sie seitdem unablässig vermehrt und jetzt einen grossen Posten stattlicher Pflanzen besitzt, die die Firma J. C. Schmidt-Erfurt erworben hat....Die durch Sportbildung erzeugte goldgelbe Farbe ist somit durch ganz andere Faktoren bedingt als die der Herbstfärbung und hat gewiss auch mit der durch Nährstoffmangel hervorgerufenen Chlorose nichts zu schaffen, da auch üppiges Wachstum die Pflanzen nicht so leicht in die grüne Stammform zurückführt." The coloured plate accompanying the above description is entitled "*Humulus Lupulus aureus* (Goldenes Vliess)"; it shows no flowers. The plant is referred to again in *Die Gartenwelt*, x. p. 498 (1906), where the name "Goldhopfen" is proposed for it.

It seems clear from the information (given above) supplied by Messrs Dicksons that the plant distributed by them is the true *H. Lupulus aureus*. It is possible that the susceptible male golden hop which has become mixed up with the immune female golden hop in the stocks held by Messrs Bunyard and by Messrs Bide and Son is also the var. *aureus*, but I have not had the opportunity yet of comparing mature plants.

(3) A third form with "golden" leaves was brought to my notice by Mr Jesse Amos, Foreman Recorder at the Wye College Fruit Experiment Station at East Malling. This plant, which is growing in a garden at Malling, was obtained originally from Messrs J. Veitch and Sons, of Chelsea. I have not been able to obtain any information as to its origin. It is of the female sex; three cuttings taken from it in 1918-19 proved in the greenhouse during 1919 to be slightly susceptible to mildew. It is therefore different in constitution at any rate to the plant sent out by Messrs Bunyard and Messrs Bide and Son. I have not yet had the opportunity of studying mature plants of this susceptible female golden hop.

To summarise the facts: we have in cultivation in nurseries and gardens in this country three forms of the Golden Hop, viz. (1) an immune female Golden Hop; (2) a susceptible female Golden Hop; (3) a susceptible male Golden Hop, the true *H. Lupulus aureus*<sup>1</sup>.

As previously reported in 1919(2) the female "Golden Hop" from Messrs Bunyard and from Messrs Bide and Son has proved completely

<sup>1</sup> In *The Hop Farmer* by E. J. Lance (1838), p. 157, the following appears: "*Varieties of Hop*.—There is another raised by Mr W. Paine at Farnham, having the appearance of the autumnal tint of the leaves, they are always 'in the yellow leaf'; indeed their appearance, compared with the red bine, or black knots, is very striking, the one being a dark blue, while the other is a light yellow green; this variety of hop branches out very much and yields a delicate coloured strobile." This "golden" variety does not appear to have been cultivated commercially.

immune to mildew both in the greenhouse and when grown in the open in a manured hop-garden. During 1918 and 1919, 47 potted plants (from the two sources noted above) were grown in the greenhouse and repeatedly inoculated with *conidia* throughout the growing season: no trace of any infection resulted. The plants ("hills") in the hop-garden, of which nine were obtained from Messrs Bunyard and three from Messrs Bide, have all remained immune to mildew for the past three to seven years.

This immune female Golden Hop lacks sufficient vigour of growth (due possibly to its possession of yellow, instead of green, leaves) to make it probable that it will ever be suitable as a commercial variety for hop-growers. With the object of trying to obtain a suitable green-leaved hop immune to mildew, "seed" was collected and sown in 1917 from a plant of the immune "Golden Hop" growing in the hop-garden at Wye College (obtained originally from Messrs Bunyard) - the male parent being unknown. In 1918 a counting of the seedlings in the three seed-boxes was made according to the colour of the first leaves, with the following results:

| Box | Yellow leaves | Green leaves |
|-----|---------------|--------------|
| 1   | 49            | 56           |
| 2   | 63            | 59           |
| 3   | 58            | 63           |
|     | 170           | 178          |

"Yellow" included several different shades of yellow: among "green" were various shades, including pale-green, but *not* yellowish-green.

The most vigorous of the above seedlings were planted out in the hop-garden in the winter of 1918-19, and during 1919 it could be observed that some seedlings were green-leaved (sometimes dark green) and some yellow (or "golden") leaved.

Other seedlings of the same origin were tested for susceptibility to mildew. These consisted of 68 seedlings raised from one plant of the Golden Hop (obtained originally from Messrs Bunyard) and 37 seedlings from another plant of the same origin. These seedlings were 2-year-old plants, non-flowering, in pots, and were kept during 1919 in the greenhouse and constantly subjected to inoculation by *conidia* throughout the season. Their behaviour towards the mildew was as follows:

|                                             | Immune | Susceptible |
|---------------------------------------------|--------|-------------|
| Seedlings of plant 1 ...<br>(Ref. no. 1/17) | 47     | 21          |
| Seedlings of plant 2 ...<br>(Ref. no. 3/17) | 25     | 12          |
|                                             | 72     | 33          |

Among the 21 "susceptible" seedlings of "1/17" there were (1) one plant "semi-immune," *i.e.* the plant showed no infection except that on one leaf there were five tiny pale spots on which a weak growth of conidiophores occurred; (2) one plant very slightly normally susceptible; (3) two plants very susceptible; while (4) the remaining plants were normally susceptible, inclining towards the slightly susceptible side.

Among the 12 "susceptible" seedlings of "3/17" two plants were slightly susceptible, with the production of normal, small patches of mildew; one plant was very susceptible; and the remaining plants were normally susceptible.

All the "immune" seedlings in both cases were entirely immune.

Among the above 105 seedlings there was a great difference of colour of the leaf; some seedlings were as "golden" leaved as the female parent; others had a normal green leaf; and intermediate shades occurred. No attempt was made to classify these seedlings on a leaf-colour basis, as owing to culture in the greenhouse there was a tendency for the green-leaved plants to acquire a pale- or yellowish-green tint due to the special conditions. It was clear, however, that there were some plants with green leaves and resistant to mildew under greenhouse conditions.

These 105 seedlings have been planted out in the hop-garden at Wye College, with the object of investigating them in the open in future seasons as regards (1) sex, (2) colour of leaves, (3) vigour of growth, (4) susceptibility to mildew, and (5) commercial value.

(2) SEEDLINGS RAISED AT WYE FROM SEED OF THE "WILD HOP"

(*H. Lupulus*) OBTAINED FROM VITTORIO, ITALY.

In 1919 cuttings of certain seedlings of the above origin were grown in pots in the greenhouse and tested for resistance to mildew both by being surrounded throughout the season by mildew-infested hop-plants and also by direct inoculations with *conidia*. While, as in past seasons, numerous clone-plants of other seedlings of the same parentage and age and treated in the same way quickly became infested with mildew (which persisted on them throughout the season), the following seedlings proved to be immune, the entire plant remaining absolutely free from any trace of infection.

Four of the following seedlings (*viz.* Z 17, OY 18, II 24, II 30) had not been tested in this way before; the remaining 15 seedlings had shown the same resistance in previous seasons (*see* (3)).

| Ref. no. of seedling | Number of clone-plants | Ref. no. of seedling | Number of clone-plants |
|----------------------|------------------------|----------------------|------------------------|
| V 91                 | 1                      | OA 49                | 2                      |
| V 92                 | 1                      | OB 34                | 10                     |
| V 93                 | 1                      | OD 19                | 2                      |
| Z 2                  | 2                      | OR 38                | 8                      |
| Z 14                 | 2                      | OR 39                | 7                      |
| Z 17                 | 1                      | OY 18                | 2                      |
| Z 22                 | 2                      | HH 44                | 2                      |
| Z 25                 | 3                      | II 24                | 2                      |
| Z 31                 | 1                      | II 30                | 2                      |
| Z 42                 | 2                      |                      | 53                     |

All the above seedlings have been growing for several years in the Experimental Hop-garden at Wye College, and Table I shows the behaviour of each seedling, and also of four other seedlings of the same origin, towards the mildew (1) when the hop-plant is growing in the hop-garden, and (2) when a cutting is taken and grown in a pot in the greenhouse.

Table I.

| Ref. No. | Sex | 1917          |                | 1918          |                                   | 1919          |                |
|----------|-----|---------------|----------------|---------------|-----------------------------------|---------------|----------------|
|          |     | In greenhouse | In hop-garden  | In greenhouse | In hop-garden                     | In greenhouse | In hop-garden  |
| 316      | ?   | 0             | —              | 0             | —                                 | —             | S <sup>1</sup> |
| V 91     | ♀   | 0             | —              | —             | S <sup>1</sup>                    | 0             | 0              |
| V 92     | ♂   | 0             | —              | —             | S <sup>1</sup>                    | 0             | 0              |
| V 93     | ♂   | 0             | —              | —             | S <sup>1</sup>                    | 0             | S <sup>1</sup> |
| Z 2      | ♂   | 0             | —              | 0             | 0                                 | 0             | 0              |
| Z 14     | ♂   | —             | 0              | 0             | S <sup>1</sup>                    | 0             | 0              |
| Z 17     | ♂   | —             | —              | —             | —                                 | 0             | *              |
| Z 22     | ♀   | —             | 0              | 0             | S <sup>2</sup>                    | 0             | S <sup>2</sup> |
| Z 25     | ♀   | —             | 0              | 0             | 0                                 | 0             | S <sup>1</sup> |
| Z 31     | ♂   | —             | —              | —             | —                                 | 0             | S <sup>1</sup> |
| Z 42     | ♂   | —             | 0              | 0             | 0                                 | 0             | *              |
| OR 38    | ♀   | 0             | S <sup>2</sup> | 0             | S <sup>2</sup> and S <sup>3</sup> | 0             | S <sup>1</sup> |
| OR 39    | ♂   | 0             | S <sup>1</sup> | 0             | 0                                 | 0             | 0              |
| OA 49    | ♀   | —             | 0              | 0             | 0                                 | 0             | 0              |
| OB 26    | ?   | 0             | —              | 0             | —                                 | —             | *              |
| OB 34    | ♀   | —             | 0              | 0             | S <sup>1</sup>                    | 0             | *              |
| OD 19    | ♀   | —             | 0              | 0             | 0                                 | 0             | S <sup>1</sup> |
| OE 14    | ?   | 0             | —              | 0             | —                                 | —             | *              |
| OY 18    | ♂   | —             | —              | —             | —                                 | 0             | S <sup>1</sup> |
| DD 31    | ?   | 0             | —              | 0             | —                                 | —             | S <sup>1</sup> |
| HH 44    | ♀   | —             | S <sup>1</sup> | 0             | S <sup>1</sup>                    | 0             | S <sup>1</sup> |
| II 24    | ♂   | —             | —              | —             | 0                                 | 0             | 0              |
| II 30    | ♂   | —             | —              | —             | 0                                 | 0             | *              |

The figures 1 to 3 indicate the amount of mildew present; 1 = mere trace of mildew, 2 = fair amount of mildew, 3 = plant very mildewed. \* signifies that no suitable material was available at the time when the observations were made (see below, p. 304).

Before we consider the significance of the *data* collected in Table I, we must note the behaviour towards the mildew of other seedlings of the same parentage and age. First, as regards the susceptibility shown in the hop-garden. In several cases we are able to compare the behaviour of seedlings growing by the side of, and close to, the "immune" seedlings of Table I; here the factors connected with soil, manuring, climatic conditions and exposure to infection by spores of the mildew are the same, so that any difference in susceptibility that is shown must be attributed to the different "constitutional" characters of the respective seedlings.

Table II.

| Ref. No. | Sex | 1917           | 1918           | 1919           |
|----------|-----|----------------|----------------|----------------|
| Z 24     | ♀   | S <sup>3</sup> | S <sup>3</sup> | S <sup>3</sup> |
| Z 26     | ♀   | S <sup>3</sup> | S <sup>3</sup> | S <sup>3</sup> |
| Z 39     | ♀   | S <sup>3</sup> | S <sup>3</sup> | S <sup>3</sup> |
| Z 41     | ♀   | S <sup>3</sup> | S <sup>3</sup> | S <sup>3</sup> |
| Z 43     | ♀   | S <sup>3</sup> | S <sup>3</sup> | S <sup>1</sup> |
| OA 26    | ♀   | S <sup>3</sup> | S <sup>3</sup> | S <sup>3</sup> |
| OA 35    | ♀   | S <sup>3</sup> | S <sup>3</sup> | S <sup>3</sup> |
| OA 53    | ♂   | 0              | S <sup>2</sup> | —              |
| OB 48    | ♀   | S <sup>3</sup> | S <sup>3</sup> | —              |
| OD 16    | ♀   | S <sup>3</sup> | S <sup>3</sup> | S <sup>3</sup> |
| OD 18    | ♀   | S <sup>3</sup> | S <sup>3</sup> | S <sup>3</sup> |
| OD 20    | ♀   | S <sup>3</sup> | S <sup>1</sup> | S <sup>1</sup> |
| II 11    | ♀   | —              | S <sup>1</sup> | —              |
| II 31    | ♂   | —              | S <sup>3</sup> | —              |

Table II records the incidence of mildew during 1917, 1918 and 1919 on 14 seedlings growing in the hop-garden.

We see that the seedlings Z 24 and Z 26, which grew on either side of the "immune" Z 25 (and so closely that lateral shoots became intertwined) have each season<sup>1</sup> become excessively mildewed. Similarly with Z 41 and Z 43, on either side of, and as close to, the "immune" seedling Z 42; and with OD 18 and OD 20 on either side of OD 19.

We will now return to the consideration of Table I. Some further *data* are available with respect to some of the plants there tabulated.

The seedlings 316, OB 26, OE 14, DD 31 were subjected to the severest test (as regards constant inoculation with *conidia*) in the greenhouse during the seasons 1916, 1917 and 1918<sup>2</sup>, and all remained persistently immune. On being planted out into the hop-garden in the winter of 1918-19, two of the seedlings (316, DD 31) showed in the

<sup>1</sup> In 1916 also both plants were S<sup>3</sup>, while no mildew occurred on Z 25.

<sup>2</sup> See (1), p. 456; (2), p. 88; (3), p. 252.

autumn of 1919 a trace of mildew on their leaves; the other two seedlings were not able to be tested as to their susceptibility.

The seedlings V 91, V 92, V 93 all completely resisted infection in the greenhouse during the seasons 1916 and 1917; the seedlings were planted out in the hop-garden in the winter of 1917-18, and the next season (Sept. 1918) each plant showed a trace of mildew on its leaves. Cuttings taken from each plant in the hop-garden in 1918-19 proved completely resistant in the greenhouse during the season of 1919, while one of the seedlings (V 93) in the hop-garden again showed a trace of mildew in Sept. 1919.

The seedling Z 22 was susceptible to the second degree in the hop-garden in both 1918 and 1919, while cuttings taken in 1918-19 proved to be immune in the greenhouse in 1919.

The seedling Z 25 is persistently immune in the greenhouse, and is usually immune in the hop-garden, although the two seedlings (Z 24, Z 26) on either side of it become severely mildewed each season. In June 1918 inoculations with *conidia* were made on the young leaves of Z 24, Z 25, Z 26, and infection resulted only on Z 24 and Z 26<sup>1</sup>. The circumstances attending the infection of Z 25 in the hop-garden in 1919 are discussed below (p. 306).

In 1918 one bine of OD 19—a strong lateral shoot arising about 5 ft. from the ground—twined round the bines of OD 18 and produced healthy hops intermingled with the excessively mildewed ones of OD 18. In 1919 a minute trace of mildew occurred in September on OD 19.

The seedlings OR 38 and OR 39 are immune in the greenhouse<sup>2</sup>; in the hop-garden susceptibility is shown, OR 38 being sometimes infected severely<sup>3</sup>.

The seedling HH 44 has shown a trace of mould in the hop-garden each season in 1917, 1918 and 1919, yet cuttings taken both in 1917-18 and 1918-19 proved to be immune when grown in the greenhouse the next season.

The evidence appears conclusive that (1) seedlings which are immune when grown in the greenhouse may show susceptibility when grown in the open; that (2) the susceptibility shown by such seedlings in the open is as a rule slight; and that (3) cuttings taken from such seedlings after

<sup>1</sup> See (3), p. 254 for further details.

<sup>2</sup> See, however, (2), pp. 84, 86.

<sup>3</sup> In 1918 two plants of OR 38, in different parts of the hop-garden, were susceptible to the extent of S<sup>2</sup> and S<sup>3</sup> (see Table I).

the latter have grown for several years in a manured hop-garden are immune to mildew when grown in the greenhouse.

Although it seems clear from the above that the conditions of growth obtaining in the greenhouse are more favourable for the phenomenon of immunity than are those in the hop-garden, experiments have shown that it is only with seedlings of a certain "constitution" that the environment has this effect on the plant. If cuttings are taken from other susceptible seedlings (of the same parentage and age) in the hop-garden, and grown in the greenhouse, no approach is shown towards immunity. In the winter of 1918-19 cuttings were taken from the following seedlings, which had been affected with mildew during 1918 to the extent indicated: Z 24 (S<sup>3</sup>), Z 26 (S<sup>3</sup>), Z 39 (S<sup>3</sup>), OA 26 (S<sup>3</sup>), OA 35 (S<sup>3</sup>), OA 53 (S<sup>2</sup>), OB 48 (S<sup>3</sup>), OD 16 (S<sup>3</sup>), II 11 (S<sup>1</sup>), II 31 (S<sup>3</sup>). These cuttings were grown, and exposed to infection, in exactly the same way as the 53 cuttings of the 19 "immune" seedlings enumerated above at p. 298, and all quickly became infected and continued so throughout the season. Most exhibited what could be called normal susceptibility, but the seedlings Z 39, OA 26, and II 31 showed extreme susceptibility under greenhouse conditions.

In no case has any seedling of the wild hop from Italy which has proved immune in the greenhouse in any one season shown any susceptibility when tested in the greenhouse in other seasons<sup>1</sup>. Since this immunity in the greenhouse is correlated with some degree of, if not total, immunity when the plant is grown in the open, the index of reaction to mildew of hop plants in the greenhouse becomes a useful guide for the selection of mildew-resistant plants for the hop-garden.

In a previous article ((3), p. 256) cases of "semi-immunity" were recorded. Four seedlings were met with showing this phenomenon, viz. Z 15, OC 6, Z 23, and OA 33. During 1919 another "semi-immune" seedling, OD 17, was found. The behaviour of all these seedlings was studied both in the greenhouse and in the hop-garden.

<sup>1</sup> In 1918 a certain seedling (Ref. No. 8/16 I) raised from a seed collected from a plant of the "wild hop" of Canada (sent to me from Morden, Manitoba, in 1916 by Prof. W. T. Macoun) growing in the hop-garden at Wye College, remained persistently immune in the greenhouse throughout the season. This seedling was a 1-year-old plant of weak growth. In 1919 the seedling, still kept in the greenhouse, was slightly more vigorous, and produced two rather weak stems (1 ft. 9 in. and 1 ft. 6 in. in length), on most of the leaves of which small "powdery" patches of mildew appeared—the plant being clearly susceptible to a normal degree. The "wild hop" of Canada is probably *H. americanus* and the present seedling is therefore most likely of hybrid origin. A similar case to the above, where the seedling concerned was of hybrid (American) origin, has already been recorded ((3), p. 257).

The seedling Z 23, of which there were two cuttings in pots in the greenhouse, showed the nearest approach to immunity of the "semi-immune" group. The only visible sign of infection on the two plants after practically continuous inoculation by *conidia* for many weeks was the production of very small raised "blisters" or "humps," over the surface of which a very weak and evanescent growth of mycelium (never abundant enough to form a visible white layer) with a few conidiophores was produced. Thus no "powdery" patches were ever produced.

The seedling OC 6 (two plants) became more evidently affected by the attacks of the *conidia* than Z 23 was, and its leaves reacted in a very characteristic manner. The infection spots were larger, but again the mildew never produced enough mycelium to be white and conspicuous, and conidiophores were never produced abundantly enough to cause a "powdery" patch. On the death of the mildew, which soon took place, the leaves showed a distinct injury (confined to the places where the mildew had existed) in the form of conspicuous yellowish-brown blotches (closely resembling those found on the leaves of certain plants attacked by *Eriophyes* (Leaf "Blister-mites")).

With Z 15 (two plants) inoculation produced on the leaves a distinctly white and more or less "powdery" conidial patch, which, however, soon died away, exposing to view a conspicuous brown spot, composed of a group of affected epidermal cells.

The seedlings OA 33 (two plants) and OD 17 (two plants) showed also very similar infection-phenomena, but with less injury caused to the epidermal cells. These two seedlings may perhaps best be put in the susceptible class, although they show a tendency towards semi-immunity.

With the seedling BB 5 inoculation was followed by the production of small patches of mildew, white and powdery, but these patches remained small and isolated, not increasing in size and becoming confluent as on the leaves of plants showing full susceptibility.

The behaviour of the above seedlings in the hop-garden during past seasons is shown in the table on p. 303.

My field-notes for the seedling OD 17 in the hop-garden were as follows: "1917. Showed considerable resistance to mould, producing a good crop of healthy hops, while OD 16 and OD 18 (two seedlings of the same parentage and age), growing on either side and so close that lateral shoots intermixed, were so infected with mould that they produced no healthy hops. 1918. Mere trace of mould on the hops; OD 17 is obviously of quite different constitution from OD 16 and OD 18, whose

laterals bearing very mouldy hops grew in among the lateral shoots of OD 17 which bore a crop of hops practically immune from mould."

Table III.

| Ref.<br>No. | Sex | 1917             |                   | 1918                         |                   | 1919                         |                   |
|-------------|-----|------------------|-------------------|------------------------------|-------------------|------------------------------|-------------------|
|             |     | In<br>greenhouse | In hop-<br>garden | In<br>greenhouse             | In hop-<br>garden | In<br>greenhouse             | In hop-<br>garden |
| Z 15        | ♂   | —                | S <sup>2</sup>    | "semi-immune"                | S <sup>2</sup>    | "semi-immune"                | S <sup>2</sup>    |
| Z 23        | ♂   | —                | S <sup>2</sup>    | "                            | 0                 | "                            | S <sup>1</sup>    |
| OC 6        | ♂   | —                | 0                 | "                            | 0                 | "                            | S <sup>1</sup>    |
| OA 33       | ♂   | —                | 0                 | approaching<br>"semi-immune" | 0                 | approaching<br>"semi-immune" | S <sup>2</sup>    |
| OD 17       | ♀   | —                | S <sup>1</sup>    | —                            | S <sup>1</sup>    | "                            | S <sup>1</sup>    |
| BB 5        | ♀   | —                | —                 | —                            | S <sup>1</sup>    | "                            | 0                 |

There appears to be evidence, then, that the physiological or "constitutional" characters which underlie the phenomenon of "semi-immunity" remain constant for the particular seedling, just as do those which account for complete immunity or susceptibility.

The phenomenon of "semi-immunity" has been met with in other seedlings of widely different parentage.

In the case of two seedlings (now planted out in the hop-garden under Ref. nos. 222 *a* and 236 *a*) studied in the greenhouse during 1919, infection scarcely proceeded further than the formation of small "humps" or "blisters," over which a scanty growth of hyphae occurred (never white in the mass), with a weak growth of conidiophores. The mildew soon died away, and exposed to view a patch of the underlying epidermal cells which had turned brown. Exactly the same phenomenon was observed with one of the seedlings in 1918. Both these seedlings were raised from seed collected by me in Sept. 1916 from a hop-plant growing wild on the sea-cliff at Salcombe Regis, near Sidmouth, Devonshire.

Another form of "semi-immunity" was met with (under greenhouse conditions) in a seedling (now Ref. no. 256 *a* in the hop-garden) raised from seed collected in 1916 from a plant of the variety *neo-mexicanus* planted in the hop-garden at Wye College—the male parent being unknown. Here inoculation is followed by the production of a weak growth of mycelium, scarcely white or "powdery," which soon dies away, leaving pale-green or yellowish, semi-translucent patches of leaf-tissue at the places where the mildew had previously existed. I have seen somewhat the same phenomenon, although not so marked, in the case of the var. *neo-mexicanus* itself, when grown in the greenhouse.

In my last communication (3), p. 253) mention was made of a group of seedlings, five in number, which for several seasons had remained immune both in the greenhouse and hop-garden. During 1919, while clone-plants of all these five seedlings remained persistently immune in the greenhouse, two of the seedlings, viz. OD 19 and Z 25 showed in the open a very slight susceptibility. Of the remaining three seedlings, two (Z 2. OA 49) still proved immune in the hop-garden, while in the case of the other, Z 42, no young growth was available in the autumn to test its susceptibility.

The circumstances under which those seedlings which are immune in the greenhouse show in the open, in some seasons, an approach towards susceptibility are worthy of study. The susceptibility shown has been noticed in past years only late in the season, in September or early October, when the plant is commonly exposed to adverse conditions of growth such as low temperatures at night, or cold rains or mists. In order to try to obtain some evidence as to which among the various cultural conditions are the determining ones with regard to the breaking down of immunity to mildew when the plant is grown in the open, cuttings of certain seedlings (all potted up in the same kind of soil) were treated in three different ways. Those in Group I were placed in the greenhouse in the autumn of 1918 and kept there throughout the season of 1919; those in Group II were kept in the open through the winter and spring until June 2 (by which time the plants had produced shoots 2 to 3 ft. long) when they were placed in the greenhouse and exposed to infection; in Group III the plants stood in the open with those of Group II until June 2, when they were placed in the hop-garden (with the pots standing in saucers so that no food could be absorbed from the soil). The seedlings which were used may be divided into three classes: *a*, those which remain persistently immune when grown in the greenhouse; *b*, those which are "semi-immune" in the greenhouse; *c*, those which are decidedly susceptible (all S<sup>2</sup> or S<sup>3</sup>) when grown in the hop-garden. The number of clone-plants used is given in brackets.

#### Group I.—Greenhouse throughout.

- Class a.* OR 38 (8); OR 39 (7); Z 25 (3); V 91 (1); V 92 (1); V 93 (1); Z 42 (2); Z 2 (2); Z 14 (2); Z 17 (1); Z 31 (1); OD 19 (2); Z 22 (2); HH 44 (2); OA 49 (2); OB 34 (10). "Golden Hop" (from Messrs Bide (6), from Messrs Bunyard (2)).
- Class b.* Z 15 (2); OC 6 (2); OA 33 (2); Z 23 (2); OD 17 (2).
- Class c.* OA 36 (1); Z 39 (1); OA 35 (1); OA 26 (1); OA 34 (1); II 31 (1); OB 48 (1); OD 16 (1); Z 24 (1); Z 26 (1).

Group II.—Outside—later moved into greenhouse.

*Class a.* OR 38 (6); OR 39 (7); V 91 (1); V 93 (1); Z 42 (1); Z 2 (1); Z 14 (1); OD 19 (2); HH 44 (1); OB 34 (10). "Golden Hop" (from Messrs Bide (6), from Messrs Bunyard (2)).

*Class b.* OC 6 (1).

Group III.—Outside—later moved into hop-garden.

*Class a.* OR 38 (11); OR 39 (8); Z 25 (3); V 91 (1); V 92 (1); V 93 (1); Z 42 (2); Z 2 (2); Z 14 (2); OD 19 (3); Z 22 (2); HH 44 (2); OA 49 (2); OB 34 (10); Z 17 (1); Z 31 (1). "Golden Hop" (from Messrs Bide (8), from Messrs Bunyard (2)).

*Class b.* Z 15 (2); OC 6 (2); OA 33 (2); Z 23 (2); OD 17 (1).

*Class c.* OA 36 (1); Z 39 (1); OA 35 (1); OA 26 (1); II 31 (1); OB 48 (1); OD 16 (1); Z 24 (1); Z 26 (1).

The plants in Group I behaved as follows:

*Class a.* All the plants remained persistently immune.

*Class b.* All the plants proved "semi-immune" (see p. 302).

*Class c.* All the plants quickly became fully infected, OA 26, Z 39, and II 31 being noted as becoming virulently infected.

The plants in Groups II and III were examined on June 13th, up to which date they had stood together in the open outside the greenhouse; all the plants in *Class a* of both Groups were healthy; of those in *Class b*, one plant of OA 33 showed in a typical form the phenomenon of "semi-immunity," and on one plant of OD 17 there was a *very* minute "powdery" patch on two of the leaves; the remaining plants were healthy. In *Class c*, more or less numerous, small patches of mildew (from natural infection) occurred on all the plants, with the exception of OA 36.

The plants of Groups II and III were then placed, respectively, in the greenhouse or in the hop-garden.

In the greenhouse the plants of Group II, *Class a* remained as persistently immune as those of Group I, *Class a*. The experiment shows, then, that the immunity of such seedlings as these is not dependent on the plants *having been raised* under greenhouse conditions, but is maintained when plants with shoots 2–3 ft. high produced in the open are taken into the greenhouse. Similarly, the seedling OC 6 in Group II, *Class b* showed the phenomenon of "semi-immunity" when taken into the greenhouse and inoculated.

With regard to the plants of Group III, no mildew was noticed on the plants in *Class a* up to the end of September. The frosts which occurred early in October shrivelled up the leaves of many of the plants, but on October 23, when an examination was made of all the plants still possessing young green leaves, one plant of OR 38 was found to be

infected very slightly, there being a tiny "powdery" patch on the undersurface of two of its leaves. Since the eight clone-plants of OR 38 kept entirely in the greenhouse and the six clone-plants taken into the greenhouse on June 13 (of the same age and potted up in the same soil) all remained persistently immune in spite of repeated inoculations, while one of the 11 clone-plants exposed in the hop-garden to natural infection showed this susceptibility late in the autumn (after frosts), it appears safe to draw the inference that the immunity of such seedlings as OR 38 is broken down, or partly broken down, by certain climatic conditions—possibly low temperature.

Certain facts, observed in the hop-garden during 1919, with regard to the behaviour of Z 25 tend to support the above view. This seedling, Z 25, was originally planted out in the hop-garden in 1914. Each season from 1916 to 1918 it remained immune to mildew, although similar seedlings (as regards origin and age) on either side of it became severely mildewed (see above, p. 299). In 1918 young leaves of Z 25 (in the hop-garden) were artificially inoculated in June, and proved completely resistant. In 1919, for the first time in the history of Z 25, a few small mildew-patches were observed on the plant in the hop-garden; this occurred on Aug. 7. The mildew-spots were on the young leaves of lateral shoots at about five feet from the ground. The mildew-affected leaves were allowed to remain on the plant, but by September all the mildew-patches had died away on these leaves, and no mildew could be found elsewhere on this plant. In early October when the plant was examined carefully, together with some hundreds of seedlings of the same parentage—most of which were severely affected with mildew—not a trace of mildew could be found on the leaves or hops of Z 25—notwithstanding the fact that laterals of the adjacent plant Z 26 had twined round the bines of Z 25 and produced hops covered with mildew among the immune hops of Z 25. The slight susceptibility shown by Z 25 in August 1919 was temporary and was caused, apparently, by some special conditions of growth. It is most probable that these conditions were climatic. Just previously to the susceptibility being shown, there was a pronounced spell of cold, and wet or dull weather, abnormal for the time of year. As soon as normal, warm and sunny weather prevailed, the patches of mildew on Z 25 died away, without any further infections having taken place, although on other seedlings of different "constitutions" the mildew prevailed and increased up to the middle of autumn<sup>1</sup>.

<sup>1</sup> The Monthly Weather Reports of the Meteorological Office for the months of June to September, 1919, were as follows: "*June*. Sunny and Warm at first, then Cool and

Seedlings which have been raised from Z 25 have shown interesting deviations from normal susceptibility to mildew. The "seed" was collected in 1917 from the plant of Z 25 growing in the hop-garden at Wye College—the male parent being unknown. In 1919, 33 of these seedlings (Ref. no. 4/17), 2-year-old and non-flowering, were grown in pots in the greenhouse and constantly exposed throughout the season to inoculation by *conidia*. The behaviour of the seedlings was as follows:

| Immune Seedlings | Susceptible Seedlings |
|------------------|-----------------------|
| 24               | 9                     |

The immune seedlings were all entirely immune.

The susceptible class comprised seedlings showing very different degrees of susceptibility. One seedling was very susceptible and another was normally susceptible—in both cases large "powdery" patches being produced by the mildew soon after inoculation. The third seedling was very slightly normally susceptible—that is to say, the few infection-spots produced consisted of normal "powdery" patches. The fourth seedling might have been termed "semi-immune," except that occasionally effused "powdery" patches were formed. The fifth, sixth, and seventh seedlings were all similar, and were apparently "semi-immune," in the sense in which this term is used above at p. 302. The last two seedlings presented new types of susceptibility not previously found in seedlings of the wild hop. In one seedling the slight susceptibility shown was manifested by the production of scattered conidiophores diffused over the

Rainy. Temperature: In England South-East the departure from normal was as small as +0.1a. The monthly aggregates of rainfall were below the normal. *July*. Cold generally; Dull in England. The mean monthly temperature was below the normal in all districts. The rainfall was below the normal, although the shortage in England South-East was only 1 mm. *August*. Many Hot days; Rainfall moderate; Sunshine abundant. Some warm days during the first part of the month were nearly balanced by some cold ones during the latter part, so that the mean for the month in most districts did not differ very largely from the normal."

The weekly deviation from Normal of the Mean of the Temperature of the Air (in degrees Fahrenheit) at the recording stations in S.E. England nearest Wye was as follows:

|                   | June 8 | June 15 | June 22 | June 29   | July 6 | July 13 | July 20 | July 27   | Aug. 3 | Aug. 10 | Aug. 17 |
|-------------------|--------|---------|---------|-----------|--------|---------|---------|-----------|--------|---------|---------|
| Recording Station | to 14  | to 21   | to 28   | to July 5 | to 12  | to 19   | to 26   | to Aug. 2 | to 9   | to 16   | to 23   |
| Tun. Wells        | +3.5   | +1.0    | -5.5    | -7.7      | -3.7   | -3.1    | -4.3    | -2.4      | +0.7   | +6.4    | +3.4    |
| Margate           | +4.7   | +3.0    | -4.4    | -5.4      | -5.3   | -1.4    | -3.6    | -2.9      | +1.1   | +6.3    | +4.2    |
| Dungeness         | +1.7   | -1.1    | -5.1    | -5.0      | -3.5   | -5.0    | -4.1    | -5.1      | -1.2   | +1.5    | +1.3    |

There seems evidence then, for considering the temporary susceptibility shown by Z 25 at the beginning of August as an effect on the "constitution" of the plant caused by the abnormally low temperatures obtaining at the end of June and throughout July.

surface of the leaf; these conidiophores were not sufficiently aggregated anywhere to form a white "powdery" patch—indeed, in most places, they could only be seen when the leaf-surface was examined carefully in a good light. In the ninth seedling infection resulted in the production of pale blotches (scattered over the leaf) on which a weak growth of mycelium and conidiophores took place.

All the above "4/17" seedlings have been planted out in the hop-garden, so that their behaviour in the open with regard to susceptibility to mildew can be studied.

### 3. A FORM OF *H. AMERICANUS* (♂).

In 1914 Dr W. W. Stockberger, of the U.S. Department of Agriculture, sent me cuttings of an American hop, labelled 7 A, 7 C, 7 H. One plant, labelled 7 A, proved during 1918 in the greenhouse to be persistently immune to mildew. During 1919 the same plant of 7 A, together with six other cuttings taken during the winter of 1918-19 from clone-plants of 7 A growing in the hop-garden at Wye College, were exposed constantly in the greenhouse to infection by *conidia* throughout the season. All the seven plants remained entirely free from mildew. Cuttings of 7 C (two plants) and 7 H (one plant) taken at the same time from plants in the hop-garden, and treated in the same way in the greenhouse, proved susceptible—7 H being susceptible to a normal degree, and 7 C being very susceptible.

The above plants were sent to me by Dr Stockberger labelled "Golden Cluster"—which is a commercial variety of hop cultivated in the United States. While, however, the single plants of 7 C and 7 H which have flowered have proved to be pistillate and doubtless belong to the variety "Golden Cluster," all the (three) plants of 7 A which have flowered are staminate. This male plant certainly belongs to *H. americanus* and not to *H. Lupulus*, as it agrees in every way with the former species, which, as has been pointed out(4), is easily distinguished by the male inflorescence. Dr Stockberger has sent me the following information: "I am surprised to learn that the plants I sent you of my Number 7 A (Golden Cluster) all proved to be staminate. The original plant Number 7, from which cuttings 7 A, 7 B, 7 C and 7 H were taken, was obtained by me from a hop-field at Cosumne, Cal., Feb. 25, 1907. The original plant Number 7 was set in my hop-garden here at Washington, D.C., where it regularly bore good hops up until the time the clones were obtained and sent to you. At the same time the cuttings were sent to you, duplicates were re-planted

in my garden here. My garden records show that these clones did not do very well, and that at present only three plants of Number 7 A remain. These, however, are all pistillate plants and have regularly borne a few clusters of hops. You can see therefore that I am quite at a loss to account for your staminate plants under Number 7 A."

The only references that I have been able to find on the subject of the resistance to mildew shown by different varieties of hops in the United States are the statements made by Prof. F. M. Blodgett. In 1913 this author wrote(5): "Thus it happens that the disease may not appear on the Cluster hop—the leaves of which appear to be more resistant than do those of the Canada, or red-vine, variety—until flowering time, when the mildew often spreads rapidly through the yards of Cluster hops, attacking the young flowers and later the hops." In 1915, Prof. Blodgett wrote(6): "Different varieties and even different leaves on the same plant vary in susceptibility. Named in order of susceptibility beginning with the most susceptible, the New York varieties would be arranged as follows: Canada red vine, English cluster, Humphrey and native red vine. No serious injury has been noticed, so far, on the native red vine variety though planted near badly infested yards and, in some instances, scattered through yards of a susceptible variety. It is said to be a light yielder, however." In a letter, dated Feb. 4, 1918, Prof. Blodgett wrote to me as follows: "I have found in the vicinity of Milford, Cooperstown, and East Springfield, in New York State, one variety of hops, the so-called 'Native Red Vines,' which appear almost entirely immune to the mildew. I have frequently seen yards in which this variety was mixed with very susceptible varieties, where the vines intertwine in many places, and still the Native Red Vine hops remained immune. Unfortunately, however, this hop is not a very desirable variety being a rather light yielder and has not appealed on that account to the growers. In 1914 a fellow in this department attempted making crosses between this and the more desirable commercial varieties in order to secure a good variety that was immune to the malady, but unfortunately this work was discontinued and was never completed."

#### SUMMARY.

1. Several forms of *H. Lupulus* with yellowish-green ("golden") leaves exist. One form (♀) has proved persistently immune to mildew both in the greenhouse and in the open. A second form (♂) has proved slightly susceptible when grown in the greenhouse. A third form (♂)

is susceptible in the greenhouse and in the open. This ♂ form appears to be the one found originally in Germany and described under the name of *H. Lupulus aureus*. No account of the origin of any ♀ "Golden hop" has been found in horticultural literature.

2. Certain seedlings raised from the immune ♀ "Golden hop" (the ♂ parent being unknown) possess green leaves and are immune to mildew when grown in the greenhouse.

3. Different seedlings of the wild hop (*H. Lupulus*) have distinctive physiological or "constitutional" characters, which are constant under the same environment. These characters confer immunity or susceptibility, or intermediate grades of susceptibility, on the respective seedlings. The immunity is retained by the plant after four years' residence in the manured soil of the hop-garden.

4. Certain seedlings of the wild hop which show persistent immunity when grown in the greenhouse show some degree of susceptibility when grown in the open. The susceptibility shown is usually very slight. There is some evidence that this breaking down of immunity is due to the effect of certain climatic conditions.

5. In the great majority of cases, the greenhouse conditions do not have the effect of making seedlings of the wild hop immune to mildew. In the case of some seedlings extreme susceptibility is shown under greenhouse conditions.

6. The phenomenon of semi-immunity is shown by certain seedlings of various origins.

7. A form (♂) of *H. americanus* Nutt., obtained from the United States, has proved immune to mildew under greenhouse conditions. Under the same conditions several American cultivated varieties proved susceptible.

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## ON THE SEXUAL FORMS OF *APHIS SALICETI*, KALTENBACH.

By MAUD D. HAVILAND,

*Fellow of Newnham College, Cambridge.*

IN June 1919, while collecting numbers of *Aphis saliceti*, Kalt., from the willow tree (*Salix caprea*) for the study of their hymenopterous parasites, it was found that the material chiefly consisted of sexual males and females, not of parthenogenetic individuals as might have been expected at that season. It is known that this aphid differs from most Aphidinae in the appearance of the sexuales at mid-summer instead of in the autumn, and their occurrence at this season has been observed both on the Continent and in America<sup>1</sup>. But hitherto they do not seem to have been recorded in this country, and as, so far as I know, there is no detailed description of these forms, one is appended.

There is some discrepancy in the earlier accounts of this species. Von Baehr (*Archiv. Zellforsch.*, 1919), who found the sexuales in Germany in May, says that Kaltenbach and de Geer also observed their appearance in summer; but reference to Kaltenbach (*Monographie der Pflanzenläusen. Aphiden*, p. 131) shows that this observer did not find them himself, though he records that de Geer found summer sexuales of *Aphis salicis*, which from the description is certainly a synonym for *Melanoxanthus salicis*, Buckt. Von Baehr supposes that this is a confusion (*Verwechslung*) between the two species, but from de Geer's description (*Memoires*, III., 11, 76) it is possible that the latter was in fact speaking of *Melanoxanthus*. He remarks on the row of white spots on the body, "puceron du saule aux taches cotonneuses," and describes the type as "obscur viridis, tuberculis lanuginosis albis, corniculis longioribus." The long cornicles apply better to *Aphis saliceti* than to *Melanoxanthus salicis*, but the pilose white patches cannot possibly refer to the former species; and Kaltenbach, who was acquainted with both forms, accepts de Geer's *salicis* as synonymous with his own. De Geer describes the male as dark yellow. Thus the possibility suggests itself that *Melanoxanthus*, which,

<sup>1</sup> 1906. Stevens, N. M. *Carnegie Institute, Wash.*, pub. 51.

1918. Gillette, C. P. and Bragg, L. C. *Can. Ent.*, Vol. L., no. 3.

so far as is known, is likewise a monophytophagous species of the willow, may sometimes produce its sexuales in June; and if this should prove to be the case, it would be an interesting point that two species of different genera on the same host plant should both produce their sexuales at this unusual season. The sexuales of *Melanoxanthus* have not been described, though Mordwilko (*Biol. Centralbl.*, 1907, p. 533) says he found them in August and September. The life-cycle of this species requires further investigation.

Parallel instances of the appearance of the sexuales in the summer are rare. Buckton (*Monograph of British Aphides*, II., p. 149) records that he found the sexuales of *Macrosiphum muralis* on *Lactuca* in the first week of July, but the females had then no eggs; and Koch says that the males of *Myzus persicae* occur in May, but, as Buckton and other observers have found the sexuales of this species in the autumn, it is possible that Koch's identification was incorrect. These seem to be the only similar cases on record; but it is possible that, with further study of the life-cycles of different aphides, the appearance of the sexuales in summer will prove to be more frequent than is now supposed, and that the disappearance of some forms, which is at present attributed to the migration of a biphytophagous species to the second host plant, will prove to be part of the normal cycle of a monophytophagous species after the production of fertilised ova. If so, as is actually the case with *Aphis saliceti*, the race can have at most but two or three months of active life: the rest of the year it exists in a dormant condition as an egg.

This species is dimorphic in respect of the parthenogenetic generations. The colour ranges from dark green to orange brown with intermediate varieties. This dimorphism extends to the sexuales, but here I found that the predominant colour for males was brown, and for females green.

#### *The male.*

Apterous. Short, oval. Length = .92 mm. Breadth of abdomen = .50 mm. Head, dusky. Eyes, reddish brown. Total length of antenna = 1.00 mm., colour, dark brown, with numerous small supplementary sensoria on segments III, IV, V. Thorax and abdomen, orange brown (rarely green), with a few darker markings on the dorsum. Genital plates dusky. Cauda, pale brown (or green). Cornicles, pale brown (or green), with dark imbricated scales, length = .28 mm. Legs, pale brown, very long and stout, with stiff hairs on femora and tibiae. Tibial joints and tarsi dusky.

*The oviparous female.*

Apterous. Long, elliptical. Posterior segments elongated. Length = 1·8 mm. Breadth of abdomen = ·83 mm. Head, dusky. Eyes, brown, and somewhat deeply set. Total length of antenna = ·90 mm., colour, dark brown, without supplementary sensoria. Thorax and abdomen, dark green (rarely brown), sometimes with darker markings on the dorsum. A pair of lateral tubercles present on segments 1, 4, 6. Cauda, green (or brown). Cornicles, green (or brown), with imbricated scales, length = ·27 mm. Legs, short and hairy, pale brown, tarsi black. Hind tibiae somewhat swollen, and bearing a few minute sensoria. Each female lays from three to five elliptical eggs on the bark of the shoots, or more rarely, on the leaves. The egg, which is at first yellow and translucent, soon becomes black and polished on exposure to the air.

## PROCEEDINGS OF THE ASSOCIATION OF ECONOMIC BIOLOGISTS.

THE ANNUAL GENERAL MEETING was held in the Botanical Department, Imperial College of Science, on Wednesday, 10th December, 1919.

There were present 32 members and 15 visitors.

In the unavoidable absence of the President and the Vice-Presidents, the chair was taken by Mr E. E. Green.

The Minutes of the preceding meeting were read and confirmed.

### *Report of the Council for 1919.*

DURING the year 1919 two general meetings have been held in the Botanical Department, Imperial College of Science, one in March and the other at the beginning of July, the latter occupying two days. They were both fairly well attended and numerous exhibits were made and important papers read.

At the latter meeting the resolutions of your Council on certain proposals made by Prof. Lefroy and Mr Brierley that had been circulated to all members in this country were passed.

Arising out of these a Botanical Secretary has been appointed in the person of Mr W. B. Brierley and steps are being taken to form a permanent Committee, of which Prof. Lefroy has consented to become a member, the duties of which *inter alia* will be to look after the interests of duly qualified Economic Biologists.

The membership of the Association shows a steady and satisfactory increase. Only one member has resigned and 13 have been elected during the year. In addition to this over 60 further members for 1920 have been nominated by the Council and their names will be placed before you at this meeting. If these are elected, they will bring our total membership from all sources up to over 200, as compared with 126 this time last year.

The publication of the *Annals of Applied Biology* in common with nearly all other scientific journals of this character has been considerably delayed, but Parts II and III of Volume VI may be expected to appear almost immediately and material for the remaining part is in hand.

The enormous increase in the cost of production of the *Annals* has been a source of considerable anxiety. With a view to improving the

position the following recommendations by the Publication Committee have been approved by your Council.

(1) The reduction of the discount to American agents from 33½ per cent. to 15 per cent.

(2) The increase of the price to the public from 7s. 6d. per Part and 25s. per annum to 10s. and 33s. 6d. respectively.

(3) That an attempt should be made to obtain financial assistance from outside sources.

The Report was adopted on the motion of Dr Paine, seconded by Mr Bewley.

A statement as to the financial position of the Association was read by the Treasurer.

The names of 69 new members who had been nominated by the Council for election to the Association were read by the Secretary.

No further names having been received, the officers and Council, a list of whom had been circulated to all members in this country, were declared elected.

#### EXHIBITS.

Mr A. D. Cotton exhibited photographs received from the Office of Forest Pathology, Bureau of Plant Industry, Washington (D.C.), showing *Cronartium cerebrum* on *Quercus rubra* and *Pinus virginiana*, *Coleosporium carneum* on *Vernonia* and *Pinus palustris*, and also a fine series of the chestnut bark canker caused by *Endothia parasitica*. Some discussion took place as to the history of *Endothia* in America and the likelihood of its being introduced to other countries.

Mr W. F. Bewley exhibited specimens of the following fungi:

##### *On Tomato fruits.*

- (1) Showing a type of hard brown rot caused by *Penicillium* sp.
- (2) Showing a soft white rot caused by a bacillus.
- (3) Rot produced by *Botrytis* sp.
- (4) Late season fruit attacked by *Macrosporium* sp.
- (5) Showing "Stripe" lesions caused by *Bacillus lathyri*.

##### *On Tomato stems.*

- (6) Attacked by *Botrytis* sp. at a jagged leaf base.
- (7) "Stripe" lesions caused by *Bacillus lathyri*.
- (8) Base of plant killed by "Sleepy Disease," showing the *Diplodadium* stage.

Mr E. E. Grean exhibited specimens of *Stephanitis rhododendri*, together with rhododendron leaves injured by the insects. He remarked

that this pest was a comparatively recent introduction, but was firmly established in Surrey and some other of the southern counties. In his own garden, Mr Green had observed that injury was confined to plants of the poorer varieties, especially such as had small, hard foliage. The insects lived on the under-surface of the foliage, but their presence was indicated by a reddish brown discoloration upon the upper surface of the leaves.

PAPERS.

The following papers were read and discussed:

Mr W. F. Bewley. "Sleepy Disease of Tomato."

Mr W. E. Hiley. "A new Method of measuring the Light Intensity in Woods."

Mr F. R. Petherbridge. "The Life-history of the Strawberry Tortrix (*Acalla comariana*)."

On Thursday, Dec. 11th, 1919 a Symposium on "The Integration of Mycological Research with Practice in Agriculture, Horticulture and Forestry" was held. The chair was taken by Professor Keeble, F.R.S. There were present 44 members and 16 visitors.

## I. THE ADMINISTRATIVE PROBLEM.

BY SIR A. D. HALL, K.C.B., F.R.S.,

*Chief Scientific Adviser to the Ministry of Agriculture and  
Director-General of the Intelligence Department.*

THE problem I have to put before you this morning is that wider one of the relation between research and government departments. There has been much talk recently of the value and need of research and of the necessity for the country to take more interest in research than it has done in the past. In the past there has been little research it is true, but that little has been good and at present in our effort for reconstruction we must beware of the danger of introducing a state king stork instead of a king log.

We may assume that research will not pay its way and therefore must be supported by state funds, which of necessity means a certain amount of state supervision of the expenditure of the money. The power of the purse unfortunately confers a certain amount of control and can be made to carry with it complete control.

The Government Department, in this case the Ministry of Agriculture, has a strong technical side, which however ought to be still stronger. This is chiefly concerned with such investigation into disease in animals and plants as is required for the formulating and carrying out of the necessary regulation for such disease. For example the outbreak of disease may be isolated and so checked by the method of quarantine. This is an old idea and in the past has been carried out by the slaughter of the animals or plants, which method can be carried out without scientific advice. It is a simple process and one dear to administrators. But investigators have suggested more economical and efficient methods than the wholesale slaughter of diseased and contacts. With animal diseases there is compulsory treatment; with plant diseases compulsory spraying. These regulations are imposed on the community and there must be inspection to ensure that they have been carried out in an efficient way. We may instance compulsory spraying as a precautionary measure imposed either by legislation or by agreement as in continental vineyards. Such a measure must be imposed by a central department and it is obviously essential that this central department be adequately advised; it must therefore be in a position to carry out investigations

to determine the value of the methods recommended. This is the immediate business of the department and the department must have research workers to whom it can look for advice.

Beyond this administrative end however is the fundamental work, the pursuit of knowledge for its own sake. This is "free" research as distinguished from "administrative" research. Men carrying out administrative research often have to range so widely afield that they do not see the need for further free research, and think that all research might as well be carried out under the government department. But this is a fundamental mistake, for a government department is unfitted by its very nature to conduct fundamental research.

In the first place governmental expenditure is subject to the closest scrutiny and criticism by non-expert bodies. Research expenditure is always liable to be overhauled by bodies such as the Treasury, the Public Accounts Committee, and the Committee on National Expenditure, *i.e.* expenditure has to be justified before non-expert bodies charged with the sole task of cutting down expenses. As an example one may adduce the reports of the United States Committee on Appropriations where you may read of the sorry spectacle of the scientist trying to justify his scientific research before them. Economic research has to justify itself in the long run by results, but it should be judged by its peers.

Such a situation reacts inevitably upon the scientific man himself. In self-protection he is driven to produce hypothetical balance sheets and to advertise himself. He is tempted to take a short point of view and not only to do work which will give immediate results but to produce these results very early. Awful examples can be quoted. Agriculture progresses in yearly cycles. The first year's investigation results in a hypothesis upon which the second year's work is based, but the second year's work often wipes out the first year's hypothesis. If however under compulsion of justification a man has tied himself to his first year's hypothesis and promised results, there is much danger that the rest of the work is forced to conform to the initial misconception.

The control of fundamental research must be in the hands of some University or some kindred body which exempts the scientific man from non-technical criticism. Such a control must impose its own criticism, but this is informed and does not demand immediate results. The government department merely allocates to the research institutions certain monies and only asks a receipt to show that these have been spent properly. It is merely a cash transaction which produces a voucher which may be shown to auditors.

In the second place the staff of a government department is graded

and there are heads who are responsible for official views which must be respected. There is no opening for destructive criticism by the lower grades. Given the right personal spirit such criticism may be welcomed, but unfortunately this is not always the case, and the official view stands damning the spirit of investigation. The attitude of the young investigator must be a purely anarchical one, one of disbelief in all things and without trust in accepted views. Such spirit has no place in the rigidity of a government department and the application of a departmental organisation to a Research Institute results in difficulties. We may remember how long the official view of the Geological Department of Scotland regarding the structure of the Highlands was held after it had been renounced by almost the entire body of the Geologists outside.

We may therefore distinguish free research, the hunt for knowledge, under the supervision of Universities or kindred bodies, and administrative research in the laboratories of government departments and by government officials who accept the necessary irksome conditions, such as sudden calls to abandon their particular problem in emergency situations. Even in free research however there must be a certain supervision of expenditure involving inspection which should be generous and enlightened. But there must come a point when the state department makes up its accounts and pronounces whether it is worth while going on with the job. Again the demarcation between departmental and free research has to be left somewhat vague and there must be a frank and generous give and take between them.

The worker in the government laboratories should similarly be given as free a hand as possible. For example many regulations laid down by the administrator involve critical methods and these need investigation, work which may carry a researcher far into the field of problems having little apparent value of direct economic end. Such an overlapping may lead to a danger that claims may be staked out and this must be watched with discretion. When one considers however the small amount of research that has as yet been accomplished and the wide scope offered by agriculture, any serious waste of energy by overlapping is no great danger in this country. And besides a certain overlapping is the lifeblood of investigation, giving that strenuous opposition and real criticism which is so valuable.

Thirdly there is the organisation of research. War time experience has shown that a very great deal can be done by organisation, by the mapping out of the field of investigation and the concentration of many workers upon particular aspects of single problems. Such team work has produced much that is new in medicine. An individual or a com-

mittee states the problem and bacteriologist, pathologist, parasitologist all work to a common end. The central body receives reports, calling conferences or interviewing individual workers, making sure that people stick to their texts and finally synthesising the results. It has been suggested that the government should apply the team method to agricultural research and be itself the central coordinating synthesising agent. That the government should organise all the workers as its team, should allocate grants and problems, and gather together the results for direct economic purposes, thus eliminating waste of energy and indeterminate research merely wasting public funds. This is a specious scheme immensely attractive to administrators.

But the analogy with medical research is very imperfect. In medicine there are a very large number of workers who have advanced to the confines of knowledge. There is much material and many laboratories at their disposal, medical schools and hospitals. Further they deal with only one organism, the human being, when the individual is so valuable that great sums may be spent on investigation. But our field presents very different features and there are so few workers that the suggested team work and method of coordination are largely superfluous. Further there is not one but many sciences each equal to human medicine—animal or plant pathology, horticulture, breeding, chemistry and study of the soil, mechanical appliances and so forth, and these are too divergent for coordination to a common end. In fact team work in this realm is largely an illusion.

There are however occasions on which team work would be possible and expedient. For instance during the war it became clear from the results of scientific experiment that the later stages in the feeding of cattle were uneconomic. Yet these results were not acted upon by the farming community for the farmers were not convinced, chiefly because the results had not sufficient volume of evidence and experiment behind them. The only effective way to obtain such evidence would have been to repeat the experiments on a very much larger scale and this could only have been done by allocating the work among various institutions.

Let us turn now to the organisation proposed by the Ministry of Agriculture in dealing with plant diseases and I may say that we are hoping in the next few years to make great advances in this direction. There are still however many financial difficulties, for government grants which at first sight seem liberal compared with those given in the past turn out to be very inadequate when viewed by present day standards.

The following are the various organisations proposed by the Ministry :

(1) *Institutes*, governed by universities or bodies like the Lawes

Agricultural Trust, secure in their independence and free from government control and devoted entirely to *free* research. The state will provide the funds and of course inspect to see that the funds are spent properly.

(2) *Departmental Investigation*. Administrative research carried out by the Ministry's staff of advisers and inspectors, but never becoming a centre of fundamental research into plant pathology. For example one may compare the Ministry's veterinary laboratory at Byfleet with the proposed institute of animal pathology sketched in the Report of the Development Commission. Again, the Ministry's laboratory for administrative research in plant pathology has been placed in Harpenden in order that it may be in the closest possible touch with the free research institute under the Lawes Trust. Attached to the Ministry's laboratory there will be a flying corps of investigators who may be detailed for emergency purposes such as sudden epidemics; these will live with the disease, for successful action depends on close continuous watching. They will require a mobile equipment in order to work on the spot.

(3) *Local Investigators*. It is intended that the staffs of local investigators attached to agricultural colleges shall be strengthened and means will be devised to bring these local workers into close contact with the headquarters staff. In this connection there will be erected advisory councils comprising administrative officers, free research workers and local investigators and it is for these bodies to ensure diffusion of knowledge and combined attack in the face of emergency problems or those which may give scope for team work. There will be no compulsory or official connection between these types of workers, but only their sense of the value of cooperation, which it is hoped will be such as to build up an organisation wherein all the parts are in intimate working relationship.

(4) *Funds*. Finally it may be stated that the Development Commission has funds with which to aid individual workers where necessity arises. Unfortunately there is still a tendency for applications to be made in cases where workers are merely carrying out routine investigations from which it is obvious that little or nothing of value can come. The only remedy for this is to ensure that better men are attracted to this work and for some time this has been a chief preoccupation of the Ministry. It is hoped that this problem has been solved now that a reasonable career can be guaranteed to every man taking up such investigations. This career may not perhaps compete financially with careers in other professions, but it will be a reasonable reward and such only is desired by those who have true research at heart.

## II. THE TRAINING PROBLEM.

BY PROFESSOR V. H. BLACKMAN, Sc.D., F.R.S.,

*Professor of Plant Physiology and Pathology in the Imperial  
College of Science and Technology.*

ON the principle that one must first catch one's student before one can train him it is clear that the prospects and conditions of service in applied mycological research must be such as to attract students possessing the right qualities. Fortunately conditions in this respect are now much more favourable than they used to be. Advance in the fundamental knowledge which is the pre-requisite to rapid advance in practice can only be attained by workers of high scientific calibre. As the type of training given must bear some relation to the lines on which it is expected that mycological research will advance, I can hardly help touching on fields other than training.

A wide outlook by the student is absolutely necessary, for plant pathology touches botanical science at so many points. Early specialisation must be determinedly avoided. A general training in botany with associated sciences such as is found in most university courses must be the basis of work. This should be followed by special training in systematic mycology, special mycological technique, and plant pathology. Although the student must have a knowledge of the chief groups of fungi, it is impossible in my opinion that all plant pathologists should, as I believe it has been suggested, be competent fungal systematists. The time required to produce such a systematist is far too great, and in general such a proficiency could only be attained at the expense of a knowledge of other sides of the subject.

The number of plant diseases is so large that a student during his training cannot become acquainted with all of them. The most satisfactory way is for the student to gain a first hand knowledge of some of the important diseases in each of the chief groups of fungi, and at the same time to acquire such facility in the examination of diseased plants as will enable him to determine exactly, or approximately, the causal organism or will enable him to isolate the organism for future observation. I may perhaps be forgiven for pointing out, what is really a commonplace

—that in the matter of the determination of the nature of a disease the plant pathologist is in a more difficult position than the ordinary medical man. The doctor attending a human patient is usually able—as the result of a few questions and the observation of symptoms—to state in a few minutes the nature of the disease; it is only rarely necessary to await the discovery of the causal organism before diagnosing the case. This is of course due to the fact that the symptoms of different diseases are, usually, sharply marked in the higher animals. Many diseases of man were quite sharply characterised before the germ theory of disease arose, and to this day the germs of many infectious diseases of man are quite unknown. In plants on the other hand the symptoms are so generalised—that is, common to so many different diseases—that a disease can rarely be determined from symptoms alone. A search has to be made for the causal organism, and when it is found it may have to be grown in artificial culture so that the reproductive organs can be obtained and the nature of the organism established. Days or weeks may thus elapse before the causal organism is identified and the nature of the disease determined.

As however the diseased condition which arises is due to the interaction of the physiological processes of the host and parasite the symptoms of each disease must be different, just as the structure of the gall is different for each combination of host and insect. The trouble is that at present our methods of analysis are not fine enough, so that these symptoms escape observation. We must however look forward to the time when better developed methods of micro-analysis will enable us to classify plant diseases by their symptoms. I may be allowed this digression to indicate the importance of the physiological aspect of plant pathology.

To return to the question of training. What is more important than a knowledge of a large number of diseases is the acquaintance with the sources of information, *i.e.*, books and scientific journals, so that the student may find his way about the subject and have confidence in his power to “get up” any branch of his subject or the knowledge of any special disease.

Since in so many cases insects play a large part in the dissemination of plant diseases some acquaintance with entomology, or at least with the habits of insects which attack plants, is of great advantage. It is clear, however, that it is practically impossible to combine in the same individual a competent knowledge of mycology and a competent knowledge of entomology.

As the questions of immunity bulk so largely at the present day some knowledge of the chief results in this relation of medical bacteriology is valuable, though I for one do not hold the view that the knowledge of toxins or anti-toxins, of lysins, precipitins, and agglutinins, knowledge which has been derived from the specialised study of medical bacteriologists, is likely to give us new weapons in the attack on economic problems of plant pathology.

The days when the only weapons for dealing with plant disease were the tracing of the life-history and the destruction of the parasite at some point in its life-cycle or the prevention of infection by sprays, are now fortunately past, since in many cases the fungus cannot at present be destroyed and the use of sprays is very often impossible. The importance of immune and resistant varieties has come to the front and it has been found that such varieties can be bred or selected. The student of mycology who is to undertake investigation of practical importance must therefore have a knowledge of the results which have been obtained in this direction. One man, however, cannot combine the capacities of a plant pathologist and a plant breeder as has, I know, been expected in some of our tropical dependencies. The two workers must unite their forces and make a combined attack.

I come now to the question of the physiological aspects. Disease is abnormal physiology, so the physiological outlook is a very necessary one, and I am glad to see that the importance of this aspect has been stressed by both Dr Russell and Mr Chittenden. It has long been recognised that the environmental conditions have a marked influence on infection; this they do by affecting the physiological reactions of both host and parasite. The physiological conditions for infection and the physiological processes connected with it are a field of work in which our knowledge is still only just beginning. The fact that different kinds of manuring may markedly affect the degree of infection, and that changes of climatic conditions may even affect the development of a fungus already within the host, show clearly the importance of the physiological aspects of plant pathology. Another question of fundamental importance in plant pathology is that of the physiological differences between immune and susceptible hosts. Also the growing importance of what may be called plant hygiene in reducing the incidence of disease shows the importance in plant pathology of the physiological conditions of the host plant. It is clear from this that the student requires a knowledge of the outlook of modern plant physiology, and therefore some training in modern plant physiology is necessary, and this of course necessitates

a grounding in physics and chemistry. No attempt should be made to make of the mycologist a competent physiologist, but such training must be given as will enable the student to appreciate the physiological outlook and to co-operate with the plant physiologist.

The training of the student should include field work even before he specialises in mycology. Ordinary botanical training with its teaching by types and its broad generalisations accentuates the similarities of plants and minimises their differences. Field work corrects this view, to which all of us are prone owing to the psychological desire for simplification; for it brings home the marked differences, not only morphological but physiological, between one plant and another. In the actual mycological training there should be as much acquaintance with disease in the field as is practically possible.

Finally one may point out that a plant pathological problem has usually such wide scientific implications that commonly no one man can hope to solve a problem unaided. For the control of disease the combined attack of the mycologist, plant physiologist and plant breeder is required, in other words, team work, as the Americans call it, is essential.

Finally I would repeat that if mycological research is to develop along lines which will be of the greatest value in practice the investigator must be a man of wide outlook, one who not only will know when to call in the plant breeder and the plant physiologist but also will be able to appreciate their point of view and to combine with them in an attack on the problems of economic plant pathology.

### III. THE AGRICULTURAL PROBLEM.

By E. J. RUSSELL, D.Sc., F.R.S.,

*Director of the Rothamsted Experimental Station.*

IN attempting to integrate mycological research with agriculture the great need of the present time is to study the growing plant in the field in health and in disease, both states being regarded as the resultant of the prevailing conditions. The problem falls naturally into two parts which may be labelled the scientific and the practical, the broad distinction being that the practical problem is one for which on grounds of expediency a working solution has rapidly to be found, while the scientific problem though of equal or greater fundamental importance is subject to no such necessity and can be studied at leisure.

The scientific problem is largely one of response. Within certain limits agricultural plants are fairly plastic: by altering easily controlled external conditions wheat plants in one and the same field may be induced to send up 8 or 10 stout stalks bearing ears well set with corn; or on the other hand, only one or two stalks carrying fewer grains. They may be made to form large broad leaves distinctly susceptible to the attacks of rust, or somewhat smaller leaves less susceptible. This is well shown on the Broadbalk wheat field at Rothamsted where there are a number of plots over which the conditions are uniform excepting only in regard to one factor, the nutritive treatment, which varies from plot to plot. The experiment is continued year after year without modification so as to ensure as high a degree of accuracy as is possible. The differences in the characters of the various crops are very clear and sharply correlated with the differences in treatment: the withholding of potash, for instance, is accompanied by marked susceptibility to adverse conditions and to rust attacks. Similarly a field of mangolds (Barnfield) is divided up chess-board fashion into a number of plots on which notable differences in size, vigour, habit of growth and susceptibility to disease are induced by alterations in the soil conditions.

In the mycological problem three sets of factors are involved: the crop, the parasite, and the external conditions. External conditions can again be subdivided into soil and climatic conditions. At Rothamsted

an attempt is being made to attack the problem on the following lines. The soil is being studied from the points of view of the chemist, the physicist, and the biologist: under the last heading separate investigators have charge of bacteria, protozoa, fungi, algae, and helminths. The climatic conditions are difficult to study, but a start has been made by following up the work of Hooker at the Meteorological Office, who has indicated certain correlations between weather and crop yields and shown that the subject is susceptible of investigation. As regards methods, one of the chief necessities is the collection and interpretation of data. Here one is met by the special difficulty that there can be no clear cut start. A chemist in securing data can at any time begin anew with perfectly clean apparatus and recrystallised initial substances, whereas in agriculture there is always a previous history to take into account: the composition of the seed is affected by the state of the parent plant, and soil may show the result of treatment after the lapse of many years. One of the plots at Rothamsted is still affected by manurial dressings which were discontinued in 1870. An experiment therefore is only valid when it is done on fields of known history.

But this does not end the difficulties. Scientific investigators are brought up on the Baconian method in which all factors are kept constant except the one under investigation. This method has led to wonderful achievements in the laboratory and is insensibly adopted by workers in all branches of science. In field experiments in our uncontrollable climate, however, it cannot be strictly applied. It is true that two plots may be laid out on which all humanly executed processes such as cultivations and other treatments may be uniform with only one factor, *e.g.* the supply of a particular fertiliser, deliberately varied. But the phenomena shown by the plant are not necessarily effects of this one factor: they may be caused by a totally different factor which has resulted from the interactions of the factor under experiment with some set of soil or climatic factors adventitiously coming together perhaps for the first and last time. Fortunately within recent years a method has been evolved for dealing with cases where several factors vary simultaneously. This is the correlation method, but its application involves the use of mathematics beyond the equipment of the average scientific investigator. The method also requires considerable masses of data.

At Rothamsted the data are all examined by a competent statistician who works out the correlations between the observed effects and the various factors concerned. His results are expressed in curves or in

constants: they require for their interpretation detailed study by a competent physiologist who will watch the plants growing in the fields. Remarkably little attention has been devoted to the growth of the plant under natural conditions. A very fruitful field of investigation is opened up by the bringing together at Rothamsted of the statistician, the mycologist, and the physiologist whom we hope shortly to bring into our circle.

A serious difficulty in agricultural investigations is the education of the workers. For convenience of University organisation the realm of Nature is divided up into certain limited areas which we have labelled chemistry, botany, physics, etc., and have come to regard as in some way different things. But the lines are in us and not in Nature. A man dealing with an agricultural problem cannot remain bound by these divisions but must be able to look over the field and see it as a whole. In practice of course this implies a body of men meeting to discuss the problem, and this necessity furnishes the best argument for large central experimental stations which otherwise are open to serious objection. At Rothamsted the staff meetings held every fourteen days to discuss the work prove of great value.

The practical problem differs in several ways from the scientific problem but especially in the degree of urgency. The investigator is asked what he can do to save a particular crop: he must therefore find a solution quickly if he is to afford any help at all. Further, there is an economic factor from which the operations of the medical investigator are entirely free. A grower fixes tolerably sharp limits beyond which he is not prepared to pay for cures for crop diseases.

Experience at Rothamsted shows that the investigation of practical problems is best made at smaller sub-stations set up in the midst of a group of growers particularly concerned. In that way workers specially interested in practical applications can obtain abundant scope for their activities both in supply of material and opportunities for experiment. The central research station gains because it is relieved of work for which it lacks special equipment, thus allowing greater concentration on fundamental problems: it further gains enormously because deductions from the results of its investigations can be tested on a larger scale under different conditions by friendly and perhaps rather candid critics. The close association between Rothamsted and its daughter-station in the Lea Valley is of great advantage to the workers on fundamental problems at Rothamsted. This station was set up to study the problems of the intensive grower under glass, largely producing tomatoes and

cucumbers. General principles are taken from Rothamsted or elsewhere, deductions are made bearing on the particular problems of the growers, and then tested on the large scale. The management is vested in a joint committee of scientific men and practical growers, the former being responsible for the programme and the latter for the finance. A mycologist, an entomologist, and an advisory officer have all been appointed: these are all good posts such as any young investigator could accept without loss of self respect.

There is a new spirit abroad among farmers and growers which is of happy augury for the future: it invites cooperation and welcomes the aid of science: nor does it wish only to receive; it is prepared to help scientific work in any way within its power. But as the farmer is often inarticulate it becomes the business of the workers at the sub-station or in the county area to state his problems for him and if possible to put them into such form that they can be investigated. Unfortunately problems in agricultural science are complicated by the multiplicity of the interacting factors: for this reason they are rarely susceptible of the clear cut statement dear to the heart of the pure research worker.

The practical problems in plant disease differ sharply from those presented to the horticulturist and the human doctor: the farmer's plants are so numerous that he cannot hope to give them individual attention but can only treat them in the mass. The elucidation of the phenomena of disease resistance, the study of the effect of environmental factors, and the breeding of resistant varieties, form the best avenues for approaching these problems. In essential principles the work has more in common with that done among human beings on Public Health and Eugenics than with curative medicine. The ultimate aim should be the avoidance of disease.

#### IV. THE HORTICULTURAL PROBLEM.

BY F. J. CHITTENDEN, F.L.S., V.M.H.,

*Director of the Royal Horticultural Society's Gardens.*

THE subject to which I have to address myself is the method by which the results of research into the causation and treatment of plant pathology may be built into general horticultural practice, where the attacks of bacteria and fungi upon cultivated plants growing under horticultural conditions are concerned.

In considering such a subject the mind naturally turns to a survey of earlier attempts in this direction, and seizes upon what appear to be causes of partial failure in the past; and it is largely upon this survey that the remarks that follow are based.

Both Professor Blackman and Dr Russell have traversed parts of the ground which a full treatment of my subject should cover and it is therefore unnecessary to enlarge upon points they have dealt with.

In preparing their campaign of integration mycologists must remember that the problems involved are not only mycological, *i.e.*, belonging to an intimate study of the organisms involved. This study cannot be too intimate and thorough, and it must include an enquiry into the powers of adaptability possessed by the parasite, and also into the range of variation existing or potential within its specific limits. Besides this, the nature of the pathological conditions set up in the host call for study. Further, as is well known, the incidence of disease in plants is dependent to a great extent upon the temporary or permanent environment of the crop, using the term environment in its largest sense. Before mycological results can be thoroughly relied upon, the conditions that favour, as well as those that discourage, the attack of the parasite upon the host must be known, and the range of variation in susceptibility to attack must be studied. Even with the commonest diseases of plants our knowledge is only partial at present, and it would tax the powers of most mycologists to the breaking point if they were called upon to say whether such and such a method of apple-growing would, with absolute certainty, avoid the incidence of even so well known a disease as the common "canker." They could more easily say what would conduce to the attack.

The special problems of the mycologist are, therefore, part only of the matter. The study of plant diseases in its entirety belongs really to

the realms of the plant-physiologist, and he may better call to his aid the mycologist to make a special study of the parasite, and the student of plant-relationships and plant-breeding, than that the mycologist should call in the aid of the physiologist. The physiological is the larger problem, and the mycologist should look upon his special task as a branch of the physiological problem. He should, indeed, view his task from the physiological standpoint, and base his work upon a thorough knowledge of physiology.

It is clear that even so far (and this is not all) the problem is one that calls for team work, for no one man can hope to tackle by himself all sides of the problems involved, though one man here and there may be able to co-ordinate the results of all the many lines of work that need to be followed up.

The points so far touched upon are general but there are some special to horticulture, and they on the one hand help to minimize the special difficulties of that art and on the other to increase them. The conditions of cultivation in the garden are, on the whole, more under control, and more artificial (in the sense that they are more "made") than in agriculture or forestry. They are therefore more capable of modification than are those of the field or the forest. The horticulturist aims to secure very large returns from a given area as compared with the agriculturist: his methods are intensive. Furthermore the agriculturist grows only a few adaptable kinds of plants and these in great numbers, while the horticulturist grows many kinds and necessarily attaches great importance to the well-being of every individual; many of these kinds, too, are of limited adaptability. The horticulturist's work entails the frequent removal of growing plants from place to place, sometimes over long distances, and thus increases the danger of carrying disease from place to place. The guarding against the contraction of disease is not so dependent upon one individual's efforts as in agriculture—it is dependent upon the vigilance of several independent persons and the dangers are therefore multiplied.

The task before the individual who attempts to integrate the results of mycological research with horticultural practice are therefore, in any particular case, on the one hand easier and on the other more difficult than in agriculture. He must devise methods of avoidance or of securing absolute immunity which all concerned may be able to adopt, or of preventing attack in the presence of danger, or of lessening the damage in the case of an attack; and in addition he must bear in mind that the treatment must be economical and such as the crop will bear. That is to say, the cost of treatment must be such that the increase in value of the crop resulting will more than balance the extra outlay.

The condition of knowledge in the country among the general public, and even among those who may be reckoned his special clientele, being what it is, he has also at times to awaken the horticulturist to a sense of danger and of loss likely to follow neglect of disease in crops, and this not only on the particular grower's own account but also on account of other persons engaged in similar industries; further he will often have to overcome prejudice as well as inertia in the direction of securing the adoption of the necessary measures of control.

It is clear that to secure these ends the man best fitted for the work will be one who can secure the confidence of practical horticulturists. Comparatively few of the latter can be expected to have either time or opportunity thoroughly to study plant diseases and their treatment; their business is mainly with the art and craft of horticulture—the growing and use of plants for their several purposes. Means to the integration may, however, be found by personal contact between the researchers and the growers. This is the best method and the researcher into avowed practical problems who takes no part in education is apt to become as barren as the teacher who takes no part in or note of current investigation. The widest public can be reached by writing in accessible periodicals or by popular books, but the writing must be clear and in simple straightforward English. The use of technical terms should be reduced to a minimum, but not avoided at the expense of accuracy, and it must be kept clearly in mind that the public whom it is desired to reach have had, as a rule, no opportunity of attaining even the rudiments of the special knowledge which the writer possesses.

Many of the leaflets published from time to time appear to fall short of their purpose because they are written to serve more purposes than one. For these, which are to go to the purely practical man who may be entirely ignorant—and it is to be borne in mind that the troubles of the allotment gardener's cabbage patch are as serious to him as are those of the apple orchard to the fruit-grower—a plain statement of the symptoms of a disease and of the methods of prevention and control is all that is desirable. Those who wish to know more may with advantage be referred to fuller papers. Argument in such leaflets is out of place and technicalities should be strenuously avoided.

Legislative measures may be used as an educative force and so used are likely to have greater value than when made the cloak for protection. And last, but by no means least, demonstration gardens accessible to all, where approved preventive and remedial measures may be seen in operation, will have an enormous influence in effecting the purpose which is the *raison d'être* of this Conference.

## V. THE FORESTRY PROBLEM.

BY PROFESSOR W. SOMERVILLE, M.A., D.Sc., D.Æc.,

*Sibthorpeian Professor of Rural Economy, Oxford.*

I UNDERSTAND that the object of this Conference is to attempt to effect an improvement in the co-relation between research and practice, and that my part in the programme is to examine the subject in its relation to Forestry.

The first reflection that occurs to me is this, that while Forestry, Horticulture and Agriculture are essentially alike in principle, in so far that all are immediately concerned with the conversion of air, soil and water into vegetable products, forestry differs from the others in these respects, (*a*) that its returns are long-deferred, (*b*) that the annual value of its out-put per acre is relatively small, (*c*) that its operations are conducted in less accessible areas, and (*d*) that its crop (trees) is physically less amenable to prophylactic or curative treatment and control. To illustrate the last point, let us compare a typical disease of a crop in field or garden, say Finger and Toe, with such a disease of trees as *Chrysomyxa abietis*. I do not say we know all about Finger and Toe, but we seem to know enough about it for all practical purposes. It can be prevented (*a*) by the avoidance of the infection of fresh areas through the agency of parts of diseased plants, including contaminated manure and soil, (*b*) by attention to cultural details, (*c*) by the use of an antiseptic substance such as lime, and (*d*) by the cultivation of resistant varieties of particular cruciferous crops. But in the presence of *Chrysomyxa abietis* one feels almost helpless. If one may take the order of its records as an indication of its progress in this country, it seems to have started in the valley of the Dee in Aberdeenshire, from which it spread into Kincardineshire, then it appeared in Perthshire, and more recently it has been recorded in Northumberland. I do not suggest that the spread of this disease is likely to threaten the spruce with destruction, though, through loss of foliage, trees that are attacked do suffer in growth and may succumb. I only mention it as an instance of a forest-tree disease which some ten years ago, so far as we know, was confined to a limited area, from which it has spread over a wide stretch of country, and in the

presence of which we seem helpless to apply preventive measures. All trees subjected to infection do not in this case contract the disease, nor do they in respect of larch disease, *Nectria cinnabarina*, *Melampsorella caryophyllacearum* and other leaf and stem parasites which could be mentioned. Evidently, therefore, there are immune strains amongst the host-plants of certain tree fungi, which suggests the idea of attempting to raise resistant varieties by the application of the laws of breeding which have given good results, with the promise of even better, in the case of field and garden crops. But, here again, we are up against not a fundamental but the practical difference between trees and other crop-plants, namely, that in the latter the period of seed to seed—a generation—is often but a year, whereas in the former it is seldom less than a quarter of a century. Then, again, in the case of at least one highly important field and garden crop—the potato—having raised your immune variety from seed you have the prospect of a commensurable return through years of vegetative reproduction. Although such propagation is not unknown in forest practice (*e.g.* willows and poplars, to some extent limes and elms) it is excluded in the case of most forest trees, which either fail to strike as cuttings, or are hard and costly to propagate as layers, and, at the best, turn out to be mis-shapen undersized individuals. But something can certainly be done in this direction by the exercise of scrupulous care in selecting sound individuals as seed-yielding plants, in the hope that immunity may be a Mendelian character, and that the particular plant may be a homozygote, and that all or most of its ovules may have been fertilised by the pollen of a similar individual. And not only should the seed-collector keep predisposition to disease in view, but other undesirable characters are also transmissible by inheritance, such as feeble growth, twisted fibre, crooked and gnarled stems, and excessive tendency to produce branches, with the consequent result of knotty and inferior timber. These characters are latent in the germ cell. When one sows a batch of tree seed in a nursery, one has the experience of finding that, in say four years, a proportion of the plants are much taller, and a proportion much dwarfer, than the others, and one might be inclined to conclude that this state of things was the result of the external conditions of growth on the particular individuals. No doubt this cause can operate, but it is much less influential than has been supposed. In point of fact it has been proved that the cell elements of dwarf individuals are shorter than those of robust growth, and that the quality of vigour is innate, and is probably a Mendelian character. The question has an important bearing on economic forestry, inasmuch as

it is a great mistake to purchase plants by size rather than by age. It is also an advantage to stock an area with many more trees than can find room in even early middle life, for thereby one has the opportunity of selecting robust individuals to stand for the final crop, and in this way the financial returns are much improved. Even in respect of improvement by accidental or deliberate breeding, there is the great difference between agriculture and forestry, in that whereas agricultural plants are, with hardly an exception, hermaphrodites, trees are with few exceptions unisexual. Self-fertilisation, with the opportunity it gives of perpetuating pure strains, while the rule in agricultural crops, is comparatively rare in trees. It is impossible in *Salix* and *Populus*, and more or less of an accident in the case of such important genera as *Quercus*, *Pinus*, *Picea*, *Larix*, *Abies*, and many others.

While impressed with the special difficulties of Research in forest mycology I am far from suggesting that there are not many hopeful lines that may be pursued. Take, for instance, that most serious pest *Peridermium Strobi*. I will not dwell upon its easily avoidable introduction to North America, where it is threatening the existence of the most important single lumber species of the North American continent, the White or Weymouth Pine. But even in this country its biology is something of a mystery. Its Cronartium stage on *Ribes* is supposed to be dependent on fresh annual infection with aecidiospores produced by the Weymouth Pine, and yet we are assured by competent observers that in the East of England this Rust occurs abundantly on currant bushes many miles removed from the opportunity of aecidial infection. The question one would like answered is this, is such infection actually produced by aecidiospores, borne by the wind or in some other way, or is it due to uredospores hibernating in fallen leaves? I know of no analogy in support of the latter suggestion, for although Rust of wheat can exist away from the Barberry, it seems to be proved that in this case the uredo stage survives the period between one crop and the next on what the Americans call "volunteer" plants, which are usually not difficult to find in neglected corners, on manure heaps, and in other places. Then, again, in America it has been observed that outbreaks of the aecidial stage occur sporadically many miles away from the infected *Ribes*, and it is suggested that the sporidia or, it may be, the teleutospores are borne on the bodies of caterpillars of the Gypsy Moth, which are said to be wind-borne over long distances. But the difficulty is to reconcile this statement with the fact that in Bagley Wood near Oxford there is a plantation of Weymouth pines whose North margin comes close up to

a cottage garden which contains *Ribes*. Practically all pines in the outer row close to the garden are infected, but directly you get into the wood even for 10 yards the disease is visibly less frequent, while 100 yards away there is no infection at all. The occurrence of the disease on the Pines is here evidently dependent not only on proximity, but on very close proximity to the teleuto host, and yet teleutospores or their sporidia, one would think, must be easily carried by wind, insects, or birds over the 100 yards of intervening space, much more easily in fact than would be the transference of aecidiospores across miles of country in East Anglia. As a matter of fact Brefeld gives 1-2 days as the usual duration of vitality in the case of aecidiospores, whereas teleutospores, as a rule, pass the whole winter as such and germinate in the following spring. It is the teleutospores, therefore, rather than the aecidiospores, that one would expect to be capable of withstanding the vicissitudes of a long passage through the air, and yet this conclusion does not seem to be supported by experience.

The integration of research, mycological and other, with the practice of forestry may be regarded from several points of view. There is, first of all, the question as to the relationship of research to practice. It is only when such relationship is aggressively obvious that some people take an interest in research at all. If only research is to be undertaken whose practical bearings are at once self-evident, then we may say goodbye to all progress of the type which persists and endures. It is a mere platitude to say that some of the biggest advances in industrial methods have emerged as side-issues in purely theoretical investigations. Do not therefore let us discourage research, for instance, into the constitution of the cell-wall; it may perhaps unexpectedly throw light on methods of impregnation with preservative materials, a subject of great and growing importance in view of the diminishing supplies of timber. Or, again, the forester does not take much interest in the initial stages of a research which may be concerned with the technical details of the hybridisation of two species of poplar, but he is not slow to appreciate the results when he is presented with a new variety which gives him a volume-yield per acre 50 per cent. greater than he has ever known before.

Another aspect of the subject is concerned with diffusion of knowledge—the bringing home to the practitioner of the results of scientific teaching and research. This is a difficulty in all industries, but particularly in forestry. In a large industrial concern there are always men associated with the management who are quick to appreciate suggestions, and who have the opportunity to test them in practice. Even in agriculture the

farmer has the power to reorganise his rotations and cultivations, to test new crops or new varieties of crop plants, to secure new manures or to revise his manurial system. In the case of the forester the situation is somewhat different. He is slow to change his methods because he is dealing with a crop which may not mature for a century, and a mistake on his part cannot be corrected in a year or two. Moreover, he is rarely in a position of sufficient independence to have the power to adopt drastic modifications even were he qualified by training to make large decisions. It is really the owner who should be educated in scientific methods so that he may intelligently direct the management of his woodlands. There is no doubt that a great change for the better has, during the past 20 years, come over the outlook of many estate owners in respect of their woodlands. This body may still be small and select, but it will grow, and it contains men of quick intelligence who are keen and alert to appreciate all that science can show them. At the moment we are at the parting of the ways in respect of forestry. We are witnessing the break-up of large estates, and the passing of much of the land, including woodlands, into the hands of smaller owners. Judging by what has happened in Ireland under somewhat similar circumstances the new owners, many of them farmers, are not likely to take much interest in their plantations except in so far as they can be converted into cash. But simultaneously with this change of ownership we have seen the creation of a Forestry Commission which is charged with the duty of extended afforestation, and the improvement of existing woodlands. I imagine therefore that in the near future we shall see extended provision made for the supply of scientific advice to woodland owners, and probably also schemes of co-partnership between the State and the individual. In this way the relationship between research and practice should be rendered much closer, and, especially so, as the Commission is likely to take steps to encourage, or even directly to undertake, forestal investigation and education. Then, again, the Commission is pledged to acquire large areas of land for fresh afforestation, and the advantages of scientific practice as illustrated in the State forests will react on the management of private areas.

At no time were class rooms and laboratories so crowded with prospective landlords as at present, and it is the general experience that these new students are imbued with an earnestness and keenness that is most stimulating to their teachers. Only a small proportion of them will become investigators in the narrower sense of the term, but all of them it is hoped, will be sufficiently immersed in the scientific atmo-

sphere to know what research means, and to appreciate its bearings on progress in agriculture, horticulture and forestry. The future landowner must take a much closer interest in his land than has generally been the case in the past, and his interest in his woodlands must be economic and scientific rather than hereditary, sporting and aesthetic. Then below the landowner there is the forester, and already, I understand, the attention of the Commission is being directed towards schemes of a thorough-going character for his education. It is, in fact, to the improvement of education all round that we may most hopefully look for enhanced appreciation of science, and when this advance has been secured the integration of research with practice will be a natural and inevitable consequence.

## VI. GENERAL DISCUSSION.

Sir DAVID PRAIN (*Director of the Royal Botanic Gardens, Kew*).

I have been asked to say something about the scope and functions of the Imperial Bureau of Mycology in its relation to the activities of Economic Biologists and to the already existing research institutions. I can only state that in all these things its part will be like that played by the Imperial Bureau of Entomology. As you are aware some ten years ago this Bureau was founded by the Entomological Committee and since that time it has, under the directorship of a member of this Association, developed in a most extraordinary manner. We hope that the Imperial Bureau of Mycology may be equally successful. The intentions underlying its foundation are similar as will be its functions, and we hope that its value to economic biology will be equally great.

E. S. SALMON (*Agricultural College, Wye*).

After listening to the papers which have been delivered this morning, two things will be present in all our minds. The first is the wide scope of economic mycology, and the second the need and value of conferences such as this.

It is interesting to look back on the progress of economic mycology during the last fifteen or twenty years. The practical man has learned how to deal successfully with disease owing largely to descriptions of the fungus and control measures written in simple language. The availability of such technical knowledge to the practical man is very recent, and one may instance the ignorance fifteen years ago of the Kent apple grower regarding Apple Scab. The leaflets published by the Ministry of Agriculture mark a great advance in the diffusion of knowledge and one may now be thankful that these leaflets are safe on the scientific side. The question has been raised whether there should not be two kinds of leaflet, one for the less and one for the better educated grower, but the present issues are certainly not too technical for the farmers and fruit growers of Kent.

Detailed knowledge is essential to practical control of the disease. The life-history of the species is not sufficient, for there are physiological species within the morphological species as in the case of the *Monilia*

causing the Brown Rot of fruit, and investigation of these physiological differences is of the most direct practical importance to growers.

The history of the American Gooseberry Mildew is very interesting from our point of view, for little was done to educate opinion until legislation came into force. The year 1907 was memorable in that the Diseases of Insects and Pests Act then came into force and the working of this Act and the inspection by the Ministry Officials has been of great educational value.

There are certain other steps to which I may refer. At a fruit growers' conference at Wye a fine-spray American nozzle was exhibited and at first one was blamed for introducing "foreign stuff." This pattern was however not patented in this country and commercial makers immediately recognised its value and manufactured copies which are now used widely. There is very much yet to be done in the improving of such mechanical objects and their operation.

I should also like to see travelling scholarships given by the Board so that students could see the best practice in disease control in other countries and bring back first hand knowledge.

Great steps have recently been made regarding the standardisation of fungicides. In 1909 a standard lime sulphur wash was first demonstrated at Wye and since that time has had wide recognition. The value of standardisation is obvious and commercial manufacturers are now themselves demanding that the washes sold should be of guaranteed specific gravity.

I agree with Professor Blackman that the physiological point of view is essential in our subject, but equally imperative is field experience not only of the crops but of the growers. A grower with a diseased plantation may not ask how he shall treat the disease but what will be the effect of pigs on the land. One must not only have a knowledge of fungi but a wide experience of the potentialities of the host plants.

**F. T. BROOKS** (*Botany School, Cambridge*).

Plant physiology is all important and I should like to spend the next five years in this study and then return to plant pathology. Equally important is field work, for this is widely different from laboratory knowledge. Only in the field can one obtain any true idea of the epidemic spread of disease, of the relative susceptibility of varieties to disease and the fact that environmental conditions often play a more important part than the actual pathogen. A tropical pathologist of acumen suggested that a necessary preliminary to mycological work was the digging

of drains and there is much to be said for this. It is essential that the mycologist should have a sympathetic attitude to the cultivator and from his earliest stages contact with growing crops is essential. Intimate crop knowledge is imperative, for too often it is complained that the suggested remedies are worse than the disease. Treatment must be on an economic basis.

The teacher must possess a wide outlook so as to counteract the tendency to segregation of knowledge which up to a point is necessary to progress but dangerous if over-emphasised. There are bound to be the teaching aspect, the research and the advisory branches but the teacher himself must be sufficiently broad to give the students the necessary comprehensive viewpoint. Often in the laboratory there is a false perspective and much time is wasted on labouring trivialities which should be spent on big problems. Only crop and field experience enable one to see things in their right proportions.

A. D. COTTON (*Ministry of Agriculture*).

I have been asked to describe briefly the kind of administrative research which will be carried out in the Ministry's new laboratory at Harpenden, for in future there will be two laboratories situated there, the Institute of Plant Pathology controlled by the Lawes Trustees and the Ministry's laboratory. The functions of the latter may be classified under four headings.

1. *Intelligence*. This mainly concerns the plant disease survey of which one report has already been issued and one is now in the press. This deals with the incidence and relative importance of pests, primarily of agricultural plants but also of those affecting trees and ornamental plants. Full records are kept and these will be available to all interested.

2. *Advisory*. This work entails a great amount of routine correspondence but it is expected that this will be reduced when the new leaflets are widely spread. It will also comprise the exhibition of specimens, field demonstrations and propaganda.

3. *Administration*. This work is often uncongenial to the scientific man but it must be done. The regulations concern the practical grower and they must be issued in consultation with him, the scientific man safeguarding their accuracy to fact. Trade regulations must have the support of the growers.

4. *Research*. Often there are problems of immediate urgency such

as sudden widespread outbreaks of disease and these must be investigated by the Ministry's officers. There is also much research work of a tedious routine nature which must be carried out, such as control methods and spraying problems. The American Gooseberry Mildew for example has been studied for nineteen years and its control is still imperfect. In addition there are always special problems elucidation of which is very desirable and these will not be neglected. To appreciate these special points the workers need to possess the true research spirit.

Professor A. HENRY (*Royal College of Science, Dublin*).

I agree generally with Professor Somerville's remarks. I wish to point out that attacks by fungi on trees in plantations twenty, thirty or more years old may involve greater financial loss than is the case in attacks of fungi on other cultivated plants. The accumulated capital of many years growth of timber may be completely destroyed.

We know that *Pinus stobus* can no longer be cultivated in Europe on account of the destructive effects of blister rust. This fungus, carried into the United States by young trees from German nurseries a few years ago, now threatens the existence of the extensive forests of this valuable pine in the United States. *Thuja gigantea*, a tree hitherto regarded as immune from disease and cultivated considerably in Britain and Ireland, has recently been attacked by a fungus, *Keithia Thujina*, which may spread and render valueless plantations of this species made in the last twenty years. At present afforestation is carried out mainly with exotic species; some like the European larch, hazardous to cultivate on account of the canker which infests it in so many situations; other species, like the Douglas fir and Sitka spruce, up to the present free from disease, and forming the bulk of many new plantations. If disease of a similar character to those first mentioned attacks the two last most valuable trees, say in ten or twenty years time, enormous loss will be incurred by the State and by private owners of woods.

What is wanted is a number of workers in mycology, who will tackle under field conditions the problem of the attacks of fungi on our common forest trees, to refer both to old and well-known enemies like larch canker and *Agaricus melleus* and to new diseases like *Keithia Thujina*.

Afforestation, without concurrent research into disease, may turn out in many cases a disastrous failure.

**A. B. BRUCE** (*Ministry of Agriculture*).

It is essential that the research worker be assured of a reasonable reward and I may perhaps indicate the scheme which has been formulated by the Ministry to improve the prospects of those engaged in investigation. A research service is to be formed analogous to the Civil Service which will provide research scholarships and permanent posts with salaries graded to a maximum of £800 per annum, above which would be the directors of the institutes. Such a rising scale cannot ensure a Newton or a Pasteur but it is a great improvement on past conditions and marks a very definite victory for a state department wrestling with a reluctant Treasury. There is further the guarantee of a pension and it is hoped ultimately to extend such a scheme not only to research institutes obtaining government grants but to advisory workers at agricultural colleges.

*The Chairman* (Professor F. KEEBLE) referred to the share Mr Bruce had taken in winning this victory and the debt of gratitude owing to him.

A. B. BRUCE (*Ministry of Agriculture*) wished to associate with himself Professor Keeble, Sir Daniel Hall and especially Mr Dale.

**H. V. TAYLOR** (*Ministry of Agriculture*).

The first thing the mycologist must do is to study the farmer and grower, for unless he can appreciate their attitude, he is likely to possess but little influence. I should also like to emphasise the value and necessity of team work. For example 100,000 tons of potatoes were rotting in Lincolnshire and the mycologist was called in and found blight. But the matter was not so simple, for the bacteriologist reported bacterial rot following blight. Again the weather was probably much to blame, for the season had been very wet and the crop late and showing second growth, which were physiological and meteorological matters. Team work throwing light on the problem from many aspects is necessary if the farmer is to be advised accurately.

Regarding administrative problems the scientist is apt to overlook just the points which the administrator insists upon and any regulations issued must not only have a scientific basis, but be economically sound and applicable on a practical scale. In my opinion there is little hope for any real progress in mycological applications until satisfactory team work is carried out.

A. B. LISTER (*Lea Valley Experimental Station*) spoke as an advisory officer attached to a Research Station rather than as a specialised

research worker. Generally speaking the practical man has a certain contempt for the scientific man because in his experience the average scientist knows little of plant culture under commercial conditions. Practical experience is essential. No less important is compatibility of temperament, for growers include all classes of men. An ideal scheme of co-ordinated research would include central stations such as Rothamsted where fundamental principles could be elucidated; then smaller sub-stations such as those in the Lea Valley and at East Malling where particular crop problems could be dealt with. These latter should each have an advisory officer forming a connecting link between the growers and laboratories. Purely administrative officials such as the Ministry's inspector should also be in touch with some central or district laboratory. In the past there has not been sufficient cooperation. The advisory officer is comparable with the medical practitioner who is also medical officer of health for his district, whilst the laboratory is akin to the specialist. The fundamental problem in all advisory work is to gain the confidence of the grower. Having this, experiments can often be carried out in the actual nurseries under the most severe commercial conditions and these are extremely valuable, not only to the particular grower but to the industry as a whole.

G. C. GOUGH (*Ministry of Agriculture*).

The inspector must learn his facts from the crop, for it is not infrequent that a laboratory recognition of a disease is useless in the field. He must also possess much tact, for practical men are of all manners and conditions and respond very differently. The administrative regulations however apply to all growers and must therefore be simple and straightforward. They must also not be selective but treat all alike and this has sometimes not been the case. It is essential that the formulation of such orders be carried out by scientists in conference with field men, for laboratory truths do not always hold in the field. For example many "new" diseases have been described by scientists but in every case it has been found that these are really of old standing and widespread incidence and that their "introduction" or "newness" is merely due to the fact that they have been overlooked.

W. F. BEWLEY (*Lea Valley Experimental Station*).

The success in bridging the gap between the central research institute and the grower depends upon the success of the sub-station, and the success of the sub-station depends upon the scientific worker. The success

of the mycologist in such work depends upon his skill in experimental technique, his experience and his keenness for work. To this must be added a thorough knowledge and sympathy with practice. The physiological aspect of the work is of great importance and much has yet to be done with plant hygiene. If possible the worker should commence with simple problems which will give "quick" positive results ensuring the confidence of the grower. The personal qualities of the worker are all-important. He must gain the friendship of the growers, exercise much diplomacy, be impervious to the innuendos of doubting members, be extremely careful and not too hasty to advise, and possess a wholesome lack of conceit.

Finally I would emphasise the need for some kind of clearing-house for Government officials, research institutes and sub-stations, some body which would gather together the special information and knowledge possessed by each branch and circulate it for the good of all. The great value of such a conference as this is that it brings together all workers.

Miss D. M. CAYLEY (*John Innes Horticultural Institute*).

There are many abnormal conditions of plants which while not due to the action of any pathogen are yet from the practical point of view to be regarded as diseases. Such for example are the bolting of turnips, lettuce, cabbages and other plants which are a source of considerable financial loss; or the rogueing of peas and potatoes which occasion the expenditure of valuable time and money. In the elucidation of these problems of plant pathology breeding is of primary importance and the facilities for this type of work are in this country extremely meagre. The value of breeding experiments in the securing of strains immune to fungal and bacterial disease needs no emphasis but it is not always realised that its value does not cease when the immune variety has been obtained. Such plants are often low croppers and the further problem is to raise them by breeding to an economic status.

Dr J. C. WILLIS spoke from an experience of twenty years direction of tropical research stations in which the problems of plant disease are ever before one. The crops, such as tea, rubber and coco-nut, are mainly perennial and cannot be handled so easily as the annual crops in English agricultural practice. Further there are no small watertight compartments but extensive areas planted solely to tea, coffee and so forth, and diseases therefore have every opportunity of spreading on an epidemic scale.

The problem of disease control is always an economic one and the

skill required is largely that of the handling of men and money. For example many treatments have been suggested for the Coffee Leaf Disease but none which are not too expensive to apply. It is cheaper to let the plant and the disease die out, but this course only serves to spread the disease by providing centres of infection. On the other hand the speaker and Mr E. E. Green had discovered remedial treatment for cocoa canker which being simple and economically sound is extensively applied.

J. R. RAMSBOTTOM (*Natural History Museum*).

The problems of the growing plant and its relation to the environment are questions for the horticulturist and agriculturist. In plant pathology the mycologist must know the fungus and regard the disease as the result of the interaction of the host fungus complex and the environmental conditions. Economic mycology however is inclusive of more than plant disease. There is for example the relation of fungus to host in such plants as the Ericaceae or Orchideae and the problems centering around the mycorrhizal relation are of very great economic importance. There is also the further problem of the fungi present in the soil and the part they play therein.

Questions of plant disease are undoubtedly largely physiological in nature but even a competent physiologist trained in laboratory technique may meet snags in his application of such knowledge to field problems.

Finance must always play a prominent part in plant pathology, for uneconomic remedies are of no use however successful they may be under trial conditions. Finally the plant pathologist must be able to identify the common fungi he meets with and this requires a certain amount of systematic study.

Miss E. M. WAKEFIELD (*Royal Botanic Gardens, Kew*).

The plant pathologist cannot be a competent systematist but he must have sufficient acquaintance with systematic work not only to identify the pathogenic organisms but to recognise new species, and to describe them accurately so that others may recognise them from his diagnoses. Mistakes in identification have been only too frequent and much confusion has resulted.

Dr H. WORMALD (*Agricultural College, Wye*).

This conference has shown the great necessity for increasing the number of workers in plant pathology so that our problems may be investigated here. At present we are compelled to rely largely on Ameri-

can and other work not only for the diagnosis of our diseases but for recommendations as to treatment. It must however be recognised clearly that conclusions which hold in other countries do not always apply here and that if we are to obtain accurate solutions of our problems, those problems must be studied in the place where they occur. For example it was believed, accepting Woronin's conclusions, that *Monilia fructigena* was practically confined to apples and pears and *M. cinerea* to stone fruits. It has been shown however that in this country *M. fructigena* may produce cankers on plums and *M. cinerea* a blossom rot of apples. Similarly conclusions arrived at in America cannot be relied upon to hold true for England.

Furthermore cultural methods of investigation have shown that there are different physiological races of *M. cinerea*. Progress in mycology will largely result from the development of cultural laboratory methods.

Dr S. G. PAINE (*Imperial College of Science*).

This conference has evolved a very exalted idea of what a mycologist should be and the knowledge he must possess—physics, chemistry, botany, mycology, farming and so forth. Such an ideal is unattainable. There is still however one other subject of which a mycologist should have knowledge and that is bacteriology. Not only is the importance of the bacteria as causal agents of disease in plants being increasingly recognised, but the bacteriological technique is being more and more extensively adopted in experimental mycology. A bacteriological training is largely one in clean cultural method and such training should take an early and important place in the education of every mycologist.

Professor F. KEEBLE (*Botany School, Oxford*).

We have heard many schemes from people partial to one or another aspect of the problem which has been before us and this conference has been of great value in bringing together and synthesising these schemes.

There must be a directing body, a milch cow providing money. There must be large research institutes carrying out fundamental investigations and radiating from these subsidiary stations situated in commercial growing areas and concerned with the actual crop problems. There must be a light cavalry—advisors who will leave the untrammelled realms of pure research and move rapidly over the field of action. There must be county organisations, technical men who will formulate the problems and ask help in their solution, and these county organisations are an essential part in the whole. This staff of people in intimate contact with the commercial growers will arrange demonstration plots and trial

grounds, the county organisation giving the facilities for such local experimentation. Finally the Board of Agriculture will defray expenses on a pound for pound basis. The Board recognises the importance of bringing together the administrator and the research worker and the integration of both research and administration with practice. No scheme can be a final or a permanent one; it will need to be modified, perhaps reversed, but the wider the basis on which it is founded the more stable it will be.

We must recognise the great value of such conferences as this and hope that it may be the precursor of many.

The proceedings closed with a vote of thanks to the Chairman.

# LIST OF MEMBERS OF THE ASSOCIATION OF ECONOMIC BIOLOGISTS FOR 1920.

1914. ADAIR, E. W., *Department of Agriculture, Cairo.*
1920. ADAMS, Miss E. F. M., B.Sc., *Seed Testing Station, Leigham Court Rd., Streatham Hill, London, S.W.*
1908. ALCOCK, Lt.-Col. A. W., C.I.E., M.B., LL.D., F.R.S., *Heathlands. Belvedere, Kent.*
1914. ANSTEAD, R. D., *United Planters' Association, Bangalore, Southern India.*
1908. ASHWORTH, Prof. J. H., D.Sc., F.Z.S., 69, *Braid Avenue, Edinburgh.*
1914. AWATI, P. R., *Central Research Institute, Kasauli, India.*
1920. BACOT, A. W., *Lister Institute, Chelsea Gardens, London, S.W. 1.*
1914. BAILEY, M. A., 49, *Alleyn Park, Dulwich.*
1905. BALFOUR, ANDREW, C.M.G., M.D., 25-27, *Endsleigh Gardens, London, N.W. 1.*
1914. BALLARD, E., F.E.S., *Government Entomologist, Coimbatore, Madras.*
1920. BALLS, W. LAWRENCE, Sc.D., M.A., *Fine Cotton Spinners' Association, St James's Square, Manchester.*
1914. BARKER, Prof. B. T. P., M.A., *National Fruit and Cider Institute, Long Ashton, Bristol.*
1920. BAYLISS ELLIOTT, Mrs J. S., D.Sc., *Botany School, The University, Birmingham.*
1919. BEER, R., *Westwood, Bickley, Kent.*
1914. BEESON, C. F. C., *Forest Research Institute, Dehra Dun, India.*
1920. BENSON, Prof. MARGARET, D.Sc., F.L.S., *Botany School, Royal Holloway College, Englefield Green, Surrey.*
- Hon. BERLESE, Prof. Dr ANTONIO, *R. Staz. di Entomologia Agraria, Firenze, Italy.*
1919. BEWLEY, W. F., M.Sc., *Experimental Station, Cheshunt, Herts.*
1915. BIJL, P. A. VAN DER, M.A., F.L.S., *Natal Herbarium, Berea, Durban, S. Africa.*
1914. BILLINGHURST, H. G., F.R.M.S., 76, *Lebanon Gardens, Wandsworth, S.W. 18.*
1920. BINTNER, J., *Helmdange, Grand Duché de Luxembourg.*
1920. BLACKMAN, F. F., M.A., Sc.D., F.R.S., *St John's College, Cambridge.*
1919. BLACKMAN, Prof. V. H., M.A., Sc.D., F.R.S., *Imperial College of Science, S.W. 7.*
1909. BLES, E. J., D.Sc., *Elterholm, Madingley Road, Cambridge.*
1916. BOCOCK, C. H., F.E.S., *The Elms, Ashley, Newmarket.*
1920. BORTHWICK, A. W., O.B.E., D.Sc., *Forestry Commission, 25, Drumsheugh Gardens, Edinburgh.*
- Hon. BOS, Prof. Dr J. RITZEMA, *Willie Commelin Scholten, Amsterdam, Netherlands.*
1920. BOYCOTT, Prof. A. E., M.A., D.M., F.R.S., 17, *Loom Lane, Radlett, Herts.*
1920. BRADE-BIRKS, Rev. S. GRAHAM, M.Sc., 16, *Bank St., Darwen, Lancs.*
1919. BRENCHEY, Miss W., D.Sc., *Rothamsted Experimental Station, Harpenden, Herts.*
1914. BRIERLEY, W. B., *Institute of Plant Pathology, Rothamsted Experimental Station, Harpenden, Herts.*

1920. BRISTOL, Miss B. M., D.Sc., *Institute of Plant Pathology, Rothamsted Experimental Station, Harpenden, Herts.*
1914. BROOKS, F. T., M.A., *The Botany School, Cambridge.*
1920. BRUCE, A. B., M.A., *Food Production Department, Ministry of Agriculture and Fisheries, 72, Victoria Street, London, S.W. 1.*
1920. BUDDIN, W., M.A., 194, *Balfour Road, Ilford.*
1914. BURNS, W., *Office of Economic Botanist, Agricultural College, Poona, India.*
1920. CAMPBELL, A. V., *The Croft, Harpenden, Herts.*
- Orig. CARPENTER, Prof. G. H., D.Sc., *Royal College of Science, Dublin, Ireland.*
1914. CAYLEY, Miss D. M., *John Innes Horticultural Institute, Merton, Surrey, S.W. 19.*
1905. CHANDLER, S. E., D.Sc., *Imperial Institute, London, S.W. 7.*
1919. CHIPP, T. F., B.Sc., *Botanical Gardens, Singapore.*
1908. CHITTENDEN, F. J., F.L.S., V.M.H., *The Laboratory, R.H.S. Gardens, Wisley, Surrey.*
- Hon. CHOLODKOVSKY, Prof. Dr. M.A., *Institut Forestier, Petrograd, Russia.*
- †1905. CORNWALLIS, F. S. W., *Linton Park, Maidstone, Kent.*
1915. COTTON, A. D., *Pathological Laboratory, Royal Botanic Gardens, Kew.*
1918. CRAGG, P. A., *Merivale Nurseries, Heston, Middlesex.*
- Hon. CUBONI, Prof. GIUSEPPE, *Phytopathological Station, Rome.*
1920. CUNLIFFE, N., *Research Institute, School of Forestry, Oxford.*
1920. CUTLER, D. W., M.A., *Rothamsted Experimental Station, Harpenden, Herts.*
1920. CUTTING, E. M., M.A., F.L.S., *Botany School, University College, Gower St., London, W.C. 1.*
1920. DARBISHIRE, Prof. O. V., Ph.D., F.L.S., *Botany School, The University, Bristol.*
1920. DAVEY, Miss A., M.Sc., *Botany School, University College, Bangor.*
1915. DAVIDSON, J., *Institute of Plant Pathology, Rothamsted Experimental Station, Harpenden, Herts.*
1920. DEACOCK, R. J., B.Sc., *School House, Crundale, Canterbury.*
1914. DEAKIN, R. H., *Joan Cottage, Bamford, Derbyshire.*
1920. DELF, E. M., B.A., D.Sc., F.L.S., *Westfield College, Hampstead.*
1915. DOIDGE, Miss E. M., M.A., F.L.S., *Division of Botany, Dept. of Agriculture, Pretoria, S. Africa.*
1918. DOWNES, H., M.B., Ch.M., F.L.S., F.G.S., F.R.M.S., *Ditton Lea, Ilminster.*
1920. DRUMMOND, M., M.A., F.L.S., *Botany School, The University, Glasgow.*
1920. DUFFIELD, C. A. W., F.E.S., *Stowting Rectory, Nr Hythe.*
1917. ELTRINGHAM, H., M.A., D.Sc., F.E.S., 6, *Museum Road, Oxford.*
1914. EMPTAGE, W. F., 1, *Ullswater Road, West Norwood, London, S.E. 27.*
1916. EYRE, J. A. VARGAS, D.Sc., *S.E. Agricultural College, Wye, Kent.*
1909. FARMER, Prof. J. B., D.Sc., F.R.S., *Imperial College of Science, South Kensington, S.W. 7.*
1905. FREEMAN, W. G., A.R.C.S., B.Sc., *Royal Botanic Gardens, Trinidad.*
1919. FRYER, C. H., 11, *St Mary's Road, Tonbridge, Kent.*
1913. FRYER, J. C. F., M.A., F.E.S., *The Pathological Laboratory, Royal Botanic Gardens, Kew.*
1919. FRYER, P. J., F.I.C., *Ravenscar, Tonbridge, Kent.*
1918. GAHAN, C. J., M.A., D.Sc., F.E.S., *British Museum (Natural History), Cromwell Road, S.W. 7.*

1914. GAMBLE, Prof. F. W., D.Sc., F.R.S., *The University, Edmund Street, Birmingham.*
1914. GARDINER, Prof. J. S., M.A., F.R.S., *Bredon House, Selwyn Gardens, Cambridge.*
1920. GATES, R. R., B.Sc., Ph.D., F.L.S., *King's College, Strand, London, W.C. 2.*
1920. GLYNNE, Miss M. D., B.Sc., *Rothamsted Experimental Station, Harpenden, Herts.*
1908. GOUGH, G. C., B.Sc., 44, *Hazlewell Road, Putney, S.W.*
1914. GOUGH, L. H., Ph.D., F.E.S., *Agricultural Department, Cairo, Egypt.*
1905. GREEN, E. E., F.E.S., *Way's End, Camberley, Surrey.*
1909. GROOM, Prof. P., M.A., D.Sc., *Imperial College of Science, South Kensington, S.W. 7.*
1915. GUNN, DAVID, P.O. Box 1013, *Pretoria, S. Africa.*
1914. GÜSSOW, H. T., F.R.M.S., 43, *Fairmount Avenue, Ottawa, Ontario, Canada.*
1920. GWYNNE-VAUGHAN, Dame HELEN, D.B.E., D.Sc., LL.D., F.L.S., *Botanical Department, Birkbeck College, Chancery Lane, London, E.C.*
1909. HADWEN, SEYMOUR, D.V.SCI., *Dominion Experimental Farm, Agassiz, Canada.*
1914. HAMILTON, Dr. LILLIAS, *Agricultural College for Women, Studley.*
1920. HENDERSON SMITH, D. J., M.D., *Institute of Plant Pathology, Rothamsted Experimental Station, Harpenden, Herts.*
1907. HEWITT, C. G., D.Sc., F.E.S., *Dominion Entomologist, Dept. of Agriculture, Ottawa, Canada.*
1910. HICKSON, Prof. S. J., M.A., D.Sc., F.R.S., F.Z.S., *The University, Manchester.*
1920. HILEY, W. E., M.A., *Research Institute, School of Forestry, Oxford.*
1920. HILL, A. W., Sc.D., M.A., F.R.S., F.L.S., *Royal Botanic Gardens, Kew.*
1920. HOLDEN, H. S., M.Sc., F.L.S., *University College, Nottingham.*
- Hon. HOPKINS, A. D., Ph.D., *Bureau of Entomology, Department of Agriculture, Washington, D.C., U.S.A.*
1919. HORNE, A. S., D.Sc., F.L.S., F.G.S., *Imperial College of Science, South Kensington, S.W. 7.*
- Hon. HOWARD, Dr L. O., *Bureau of Entomology, Department of Agriculture, Washington, D.C., U.S.A.*
1920. HUNTER, BERNARD KEITH, *Oldfield, Swanage, Dorset.*
1914. HUTCHINSON, C. M., *Pusa P.O., Darbhanga District, Bihar, India.*
1914. HUTCHINSON, H. P., *The Laurels, Kegworth, Derby.*
- Orig. IMMS, A. D., D.Sc., F.L.S., F.E.S., *Institute of Plant Pathology, Rothamsted Experimental Station, Harpenden, Herts.*
1920. ISAAC, P. V., B.A., F.E.S., 2, *Gledhow Terrace, South Kensington, London, S.W.*
1918. JACKSON, Miss D. J., *Swordale, Evanton, Ross-shire.*
1920. JACKSON, Miss V. G., B.Sc., *Rothamsted Experimental Station, Harpenden, Herts.*
1918. JARDINE, N. K., *Peradeniya, Ceylon.*
1907. JEPSON, F. P., *Peradeniya, Ceylon.*
1920. JEWSON, Miss S. T., B.Sc., *Institute of Plant Pathology, Rothamsted Experimental Station, Harpenden, Herts.*
1920. JONES, Prof. W. NEILSON, M.A., F.L.S., *Bedford College, Regent's Park, London, N.W.*

1918. KANNAN, KUNUI, M.A., F.E.S., *Asst. Entomologist, Govt. of Mysore, Bangalore, S. India.*
1915. KEEBLE, Prof. F., C.B.E., M.A., D.Sc., F.R.S., *Botany School, Oxford.*
1920. KIDD, F., M.A., D.Sc., *Botany School, Cambridge.*
1907. KING, H. H., F.L.S., F.E.S., *Gordon College, Khartoum, Sudan.*
1907. KING, Prof. L. A. L., M.A., *West of Scotland Agricultural College, Blythswood Square, Glasgow.*
1908. LEES, A. H., B.A., *National Fruit and Cider Institute, Long Ashton, Bristol.*
- Orig. LEFROY, Prof. H. MAXWELL, *Imperial College of Science, South Kensington, S.W. 7.*
1909. LEIGH, H. S., M.Sc., *Brentwood, Worsley, Nr Manchester.*
1909. LEIPER, R. T., M.D., D.Sc., 103, *Corringham Road, Golder's Green, N.W.*
1914. LESLEY, J. W., *Emmanuel College, Cambridge.*
1915. LISTER, A. B., B.Sc., D.I.C., *Experimental Station, Turner's Hill, Cheshunt, Herts.*
1920. LLOYD, LLEWELLYN, M.Sc., *Experimental Station, Turner's Hill, Cheshunt, Herts.*
- †Orig. MACDOUGALL, R. S., M.A., D.Sc., F.R.S.E., F.E.S., 9, *Dryden Place, Edinburgh.*
1914. MCCLELLAN, F. C., M.R.A.C., F.L.S., *Director of Agriculture, Zanzibar.*
1920. McLEAN, Prof. R. C., M.A., D.Sc., F.L.S., *Botany School, University College, Cardiff.*
1920. McLEAN THOMPSON, J., M.A., D.Sc., F.R.S.E., *Botany School, Glasgow.*
1909. MANGAN, J., M.A., *University College, Galway.*
1920. MANGHAM, S., M.A., *Botany School, Armstrong College, Newcastle.*
1917. MANN, H. H., D.Sc., F.L.S., *Agricultural College, Poonah, India.*
- Hon. MARCHAL, Prof. P., *Station Entomologique, 16, Rue Claude Bernard, Paris.*
1914. MARSHALL, G. A. K., D.Sc., F.Z.S., F.E.S., 6, *Chester Place, Hyde Park Square, W.; and Imperial Bureau of Entomology, British Museum (Natural History), Cromwell Road, S.W. 7.*
1920. MASON, FRANCIS ARCHIBALD, 29, *Frankland Terrace, Leopold Street, Leeds.*
1920. MATTHEWS, Mrs D. J., M.Sc., *Rothamsted Experimental Station, Harpenden, Herts.*
1920. MELLOR, J. E. M., B.A., 51, *Onslow Square, London, S.W. 7.*
1914. MOORE, Sir F. W., M.A., M.R.I.A., V.M.H., *Botanical Gardens, Glasnevin, Dublin, Ireland.*
1920. MORRIS, Sir DANIEL, K.C.M.G., M.A., D.Sc., LL.D., D.C.L., C.M.Z.S., V.M.H., F.R.H.S., 14, *Crabton Close, Boscombe, Hants.*
1920. MOSLEY, F. O., F.L.S., *Laboratory of Plant Pathology, University College, Reading.*
1920. MURPHY, A. J., 2, *Dorset Square, London, N.W. 1.*
1914. NEAVE, S. A., M.A., D.Sc., F.Z.S., F.E.S., 24, *De Vere Gardens, Kensington, W. 8; and Imperial Bureau of Entomology, 88, Queen's Gate, S.W. 7.*
- Hon. NEUMANN, Prof. L. G., *Ecole Nationale Vétérinaire, Toulouse, France.*
- Orig. NEWSTEAD, Prof. R., M.Sc., F.R.S., A.L.S., *School of Tropical Medicine, The University, Liverpool.*
1918. OLIVE, G. W., *Grafton House, Oundle, Northants.*
1920. OLIVER, Prof. F. W., M.A., D.Sc., F.R.S., *Botanical Department, University College, London, W.C. 1.*

1910. OSBORN, Prof. T. G. B., *The University, Adelaide, S. Australia.*
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1920. PALMER, RAY, *Ingleholme, Norton Way, S., Letchworth.*
1914. PEARSON, J., D.Sc., *Director, The Museum, Colombo, Ceylon.*
1920. PERCIVAL, Prof. J., M.A., F.L.S., *University College, Reading.*
1914. PETHERBRIDGE, F. R., M.A., *Sidney Sussex College, Cambridge.*
- Orig. PETHYBRIDGE, G. H., Ph.D., B.Sc., *Royal College of Science, Dublin, Ireland.*
1914. POLE-EVANS, J. B., D.Sc., F.L.S., *Agricultural Department, Pretoria, Transvaal.*
1919. POMEROY, A. W. J., *Govt. Entomologist, Ibadan, Southern Nigeria.*
1915. PORTER, Dr ANNIE, *Zoological Department, S. African School of Mines and Technology, Johannesburg.*
- †1907. POULTON, Prof. E. B., M.A., D.Sc., LL.D., F.R.S., F.L.S., F.G.S., F.Z.S., F.E.S., *Wykeham House, Oxford.*
1920. PRIN, Lt.-Col. Sir DAVID, C.M.G., C.I.E., M.A., M.B., F.R.S., LL.D., F.R.S.E., V.M.H., *The Royal Botanic Gardens, Kew.*
1908. PRIESTLEY, Prof. J. H., B.Sc., *The University, Leeds.*
- Hon. RAILLIET, Prof., *Alfort, Paris.*
1919. RAYNER, Dr. M. C. (Mrs NELSON JONES), *University of London Club, 21, Gower Street, W.C. 1.*
1920. RENDLE, A. B., M.A., D.Sc., F.R.S., F.L.S., *Keeper of Botany, British Museum (Natural History), Cromwell Road, London, S.W. 7.*
1914. RENNIE, J., D.Sc., F.R.S.E., 60, *Desswood Place, Aberdeen.*
1910. RETTIE, T., D.Sc., 12, *Ann Street, Edinburgh.*
1914. ROBERTS, A. W. RYMER, M.A., F.E.S., *School of Zoology, Cambridge.*
1916. ROBINSON, WILFRED, D.Sc., *Department of Botany, University of Manchester.*
1918. ROBSON, ROBERT, *Institute of Agriculture, Chelmsford.*
1920. ROEBUCK, A., N.D.A., *Harper Adams College, Newport, Salop.*
1907. ROGERS, A. G. L., *Ministry of Agriculture and Fisheries, 6, St James's Square, London, S.W. 1.*
1920. RUSSELL, E. J., D.Sc., F.C.S., F.R.S., *Rothamsted Experimental Station, Harpenden, Herts.*
1920. SALISBURY, E. J., D.Sc., F.L.S., *Botanical Department, University College, London, W.C. 1.*
1914. SALMON, E. S., F.L.S., *S.E. Agricultural College, Wye, Kent.*
1920. SEARLE, G. O., B.Sc., *School of Botany, Cambridge.*
1920. SEWARD, Prof. A. C., M.A., D.Sc., F.R.S., F.G.S., *Botany School, Cambridge.*
- †Orig. SHIPLEY, Sir A. E., M.A., D.Sc., F.R.S., *Christ's College, Cambridge.*
1920. SMALL, Prof. J., D.Sc., Ph.C., F.L.S., *Botany School, The University, Belfast, Ireland.*
1920. SMITH, A. MALINS, M.A., F.L.S., *Biology Department, Technical College, Bradford.*
1920. SMITH, E. HOLMES, B.Sc., *Botany School, The University, Manchester.*
1920. SMITH, W. G., B.Sc., Ph.D., *College of Agriculture, Edinburgh.*
1913. SNELL, JOHN, *Bank Chambers, Ormskirk, Lancs.*
- Orig. SOMERVILLE, Prof. W., M.A., D.Sc., D.Cec., 121, *Banbury Road, Oxford.*
1913. SOUTH, F. W., *Agricultural Department, Kuala Lumpur, Federated Malay States.*

*List of Members*

1919. SPEYER, E. R., *Ridgehurst, Shenley, Herts.*  
 1920. SPINKS, G. T., M.A., *Agricultural and Horticultural Research Station, Long Ashton, Bristol.*  
 1919. STONE, H., *Forestry School, University of Cambridge.*  
 1920. SUTHERLAND, Prof. SCOTT, M.A., *Botany Department, University College, Southampton.*  
 1920. SUTTON, A. W., V.M.H., F.L.S., 9, *Upper Phillimore Gardens, Campden Hill, London, W. 8.*  
 1920. SUTTON, MARTIN H., F.L.S., *Erleigh Park, Whiteknights, Reading.*  
 1905. SWANTON, E. W., *Brockton, Haslemere, Surrey.*  
 1920. TABOR, R. J., B.Sc., *Botany School, Imperial College of Science, London.*  
 1913. TAYLOR, F. H., *Dalmally Station, via Roma, Queensland.*  
 1915. TAYLOR, H. V., *Ministry of Agriculture, London, S.W. 1.*  
 1914. THEOBALD, Prof. F. V., *Wye Court, Wye, Kent.*  
 1920. THOMAS, Miss E. N. MILES, D.Sc., F.L.S., *Botanical Department, National Museum of Wales, Cardiff.*  
 1920. THORNTON, H. G., B.A., *Rothamsted Experimental Station, Harpenden, Herts.*  
 1915. TREHERNE, R. C., *Agassiz, British Columbia.*  
 1920. TROW, Principal A. H., D.Sc., F.L.S., *University College, Cardiff.*  
 1913. URICH, F. W., *Board of Agriculture, Port of Spain, Trinidad.*  
 1914. VASSALL, ARCHER, M.A., F.Z.S., *Harrow School, Harrow.*  
 1920. WAGER, H. H., D.Sc., F.R.S., F.L.S., "*Hendre*," *Horsforth Lane, Far Headingley, Leeds.*  
 1920. WAKEFIELD, Miss E. M., F.L.S., *Royal Botanic Gardens, Kew.*  
 1905. WALKER, A. D., *Ulcombe Place, Nr Maidstone.*  
 1911. WALLACE, Prof. R., *The University, Edinburgh.*  
 1920. WALLER, JOHN CLAUDE, B.A., *S.E. Agricultural College, Wye, Kent.*  
 Orig. WARBURTON, CECIL, M.A., *Yew Garth, Grantham, Cambridge.*  
 1920. WARE, W. M., B.Sc., *Brookfield, Fremington, Barnstaple, N. Devon.*  
 1914. WATERSTON, Capt. J., M.A., B.Sc., *Imperial Bureau of Entomology, Nat. Hist. Museum, South Kensington, S.W. 7.*  
 1920. WATSON, W., A.L.S., *Curator of the Royal Botanic Gardens, Kew, Surrey.*  
 1920. WEISS, Prof. F. E., D.Sc., F.R.S., F.L.S., *Botany School, The University, Manchester.*  
 1905. WELLCOME, HENRY S., *Snow Hill Buildings, London, E.C. 1.*  
 1918. WEST, CYRIL, D.Sc., A.R.C.S., D.I.C., F.L.S., 7, *Colfe Road, Forest Hill, S.E. 23.*  
 1905. WILKS, Rev. W., M.A., *Royal Horticultural Society, Vincent Square, Westminster, S.W.*  
 1912. WILLIAMS, C. B., B.A., 20, *Slatey Road, Birkenhead.*  
 1909. WILLIAMSON, H. C., M.A., D.Sc., *Fishery Board of Scotland, Aberdeen.*  
 1920. WILKIS, J. C., M.A., D.Sc., F.R.S., *Beechcroft, Clarendon Road, Cambridge.*  
 1920. WILSON, MALCOLM, R.B.S., 31, *Warder Road, Trinity, Edinburgh.*  
 1914. WORMALD, H., D.Sc., A.R.C.S., *S.E. Agricultural College, Wye, Kent.*  
 1917. WRIGHT, F. S., *Ministry of Agriculture, London, S.W. 1.*  
 1916. WRIGHT, HERBERT, *Mincing Lane House, London, E.C. 3.*

† Indicates members who have compounded for their annual subscription.

## LAWS OF THE ASSOCIATION OF ECONOMIC BIOLOGISTS.

1. The Association shall be named "The Association of Economic Biologists."  
 2. The objects of the Association shall be to promote the study of Economic Biology.

3. The Association shall consist of Honorary and Ordinary Members.

4. Each candidate for ordinary membership shall be nominated by two members. Such nomination shall be approved by the Council and confirmed by a vote of two-thirds of the members present and voting at the next General Meeting.

Every member elected shall receive notice from the Secretary and shall continue a member until his written resignation shall be received by the Secretary, or until membership be forfeited under the Laws.

Ordinary Members shall pay an annual subscription of One Guinea, due on January 1st of each year, or may compound for their subscription with a sum of fifteen guineas.

All Ordinary Members on first election shall pay an entrance fee of half-a-guinea.

5. Ordinary Members shall be entitled to admission to all the meetings of the Association, to vote thereat, to present papers, to take part in discussions and to receive a copy of the Association's publications.

Each member shall be entitled to introduce personally non-members to the Association's meetings.

6. Honorary Members shall be persons, *not subjects of the British Crown*, who have contributed in an eminent degree to the advancement of the science of Economic Biology. They shall be recommended by a majority of the whole Council and elected in the same manner as Ordinary Members.

The number of Honorary Members shall not at any time exceed *twelve* and not more than *two* shall be elected in any one year.

Honorary Members shall not be liable to any payments and shall each receive a copy of the Association's publications.

Their privileges shall be the same as those of Ordinary Members, but they shall not be entitled to vote at the meetings.

7. The Council shall have power, at any of their meetings, by two-thirds of the votes of those present and voting, to terminate the membership of any member whose subscription shall be one year or more in arrears, or whose membership shall, from any other cause, be undesirable. No member whose subscription is in arrears shall be entitled to vote at a General Meeting or to receive the Association's publications, nor shall any publication be sent to a new member until his entrance fee and subscription shall have been received.

8. All meetings shall be announced by circular addressed to all Members resident in the United Kingdom. The place and time of the meetings shall be decided by the Council; ten shall be a quorum at such a meeting.

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9. An Annual General Meeting shall be held and shall ordinarily be the General Meeting falling nearest to the end of the year or as the Council shall decide.

At this meeting the order of business shall be:

1. The reading of the minutes of the previous meeting.
2. The reading of a report of the Council on the work of the past year.
3. The statement of the Treasurer.
4. The election of members.
5. The election of Officers and other Members of the Council.
6. Other business.

10. The business of the Association shall be conducted by a Council consisting of a President, not more than five Honorary Vice-Presidents, a Treasurer, one or more Secretaries, and twelve other members.

11. The Council shall nominate the Officers and other Members of the Council for the ensuing year. A list of such nominations shall be sent to all members resident in the United Kingdom at least three weeks before the Annual General Meeting. The President shall designate two Members of Council to act as Vice-Presidents.

Any Member proposing an addition to, or an alteration in, the list must inform the Honorary Secretary by letter at least ten days before the Annual General Meeting.

The nominations shall be confirmed by the members present at the Annual General Meeting and a ballot shall be taken in the event of any additions or alterations being proposed.

12. The Council may fill up any vacancy that may occur in the list of Officers and Council.

13. The Council shall meet at such times as they may determine; six members shall form a quorum.

The Council shall purchase such books, instruments, specimens, furniture and other necessities as may be required, pass the accounts and authorise their payment, and generally manage the affairs and administer the funds of the Association.

14. The Council shall appoint from the Members of the Association an Editorial Committee who shall be responsible for the publications.

15. At a Council Meeting, prior to the Annual General Meeting, the Council shall appoint one or more Auditors to audit the Treasurer's Accounts.

16. All properties of the Association, both present and future, shall be deemed to be vested in the Council of the Association for the time being, in conformity with the provisions of the Literary and Scientific Institutions Act, 1854.

17. No new Law shall be made nor any Law altered except on the proposition of the Council or the requisition of at least ten members addressed to the Honorary Secretary. The new Laws or alterations of Laws shall be proposed in writing, signed by the requisitionists and delivered to the Honorary Secretary a month before an Extraordinary General Meeting, which shall be called for the purpose.

Such proposed new Laws or alterations in the Laws shall be printed in the circular convening the Meeting, and sent to all members resident in the United Kingdom at least two weeks before the date of such Meeting.

No new laws, alterations or amendments shall be passed except by a two-thirds majority, when not less than fifteen members are present and voting.

CAMBRIDGE: PRINTED BY  
J. B. PEACE, M.A.,  
AT THE UNIVERSITY PRESS





